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Gopher Snakes and Rattlesnakes: Presumptive Batesian Mimicry

Abstract

The great basin gopher snake and northern pacific rattlesnake belong to different families of snakes yet possess similarities in coloration and warning displays. Both possess a chain of dorsal dark blotches set off by a light background coloration or white markings; when threatened, both species display a similar coiled body posture, tail motion, triangular head shape, and sound production (hissing by gopher snake and tail vibration by rattlesnake). Differences in habitat utilization and locomotion make ecological convergence to a common niche an unlikely explanation for such similarities. Rather, near geographic coincidence of ranges, high toxicity of rattlesnakes, and basic similarities in color pattern and warning display between the two species make it more likely that the gopher snake and rattlesnake are mimic and model respectively of a Batesian mimicry system.

Introduction

The great basin gopher or "bull" snake (*Pituophis melanoleucus deserticola*) and the northern pacific rattlesnake (*Crotalus viridis oreganus*) share similarities in color and warning display that suggest they represent an instance of Batesian mimicry, the venomous rattlesnake serving as presumptive model to the gopher snake mimic. The range of the gopher snake closely coincides with the rattlesnake (Stebbins, 1966) in northwestern United States. Here both are found in the Upper Sonoran and often in riparian habitats. Unlike the rattlesnake, the gopher snake climbs low shrubs and trees in search of bird eggs, young, and an occasional adult (Kardong, 1974). The toxicity of rattlesnake venom is well established (Klauber, 1956), although the bite is not always fatal (Glass, 1976; Reid, 1970). On the other hand, gopher snakes are non-venomous and even lack a Duvernoy's gland (Taub, 1976). The purpose of this paper is to describe the similarities and discuss the basis for proposing the presumptive Batesian mimicry between these two snake species.

Methods

The gopher snakes (*Pituophis melanoleucus deserticola*) and rattlesnakes (*Crotalus viridis oreganus*) compared in this study were collected in the eastern part of Washington state. Behavioral observations were made in the field and on live specimens in captivity.

Results

Coloration

The rattlesnake has a stout body, the gopher snake a longer and more slender body. The general background coloration of the rattlesnake varies between cream, yellow, gray, olive, and brown whereas the gopher snake is usually cream-colored. However, both

species possess a chain of separated dark blotches along their backs. The blotches in the rattlesnake are often set off by light or white markings and in the gopher snake by the light background coloration.

Warning Displays

1) Body posture. When encountered in the field, both species will usually withdraw. If they do not withdraw, then in the presence of humans they assume a similar pose. Both species draw their bodies into loose coils with head raised four to eight inches off the ground and directed at the human intruder. The neck is S-shaped so that the rapid straightening of these curves permits the snake to strike outward from the posterior body coils that rest on the ground. Observing this behavior in the field, gopher snakes were more prone to strike out than were rattlesnakes, but such defensive postures are common to both.

2) Tail motion. The rattlesnake, if stimulus level is high, will rapidly vibrate its tail containing the loosely interlocking cornified segments and produce the characteristic "rattling" sound. Likewise, the gopher snake vibrates the tip of its tail as well. There are, of course, no rattles present on it, but if it should come into contact with loose dried material such as leaves, a "buzzing" sound is produced.

3) Head shaping. The presence of large venom glands in the temporal region of the rattlesnake head gives it the well-known triangular shape. In gopher snakes, the head during the display is formed into a triangular shape accomplished by the active spreading of the posterior part of the jaws. This "head shaping" display in gopher snakes is usually accompanied by hissing; the display is soon lost when in captivity and after a short time does not appear as part of the warning display repertoire.

4) Sound production. The primary sound produced by rattlesnakes is by the rapid vibration of the tail. To the human ear this may sound like a baby's rattle or to some like the sound of air escaping from a gas jet. The gopher snake likewise can produce a sound with its rapidly vibrating tail but only if it should come into contact with loose, dry material. However, gopher snakes produce a hissing sound generated by forceably expelling air from the lung out the glottal opening bisected by a preglottal plate (Saiff, 1975). While hissing, the lips are parted slightly (Fig. 1) to permit escape of expelled air. Continuous hisses of up to four seconds have been recorded, followed by deep inhalation, followed by a second strong hiss, and so forth. The duration of these cycles seems to depend upon the stimulus level and customarily accompanies the other features of the warning display described above.

Summary and Conclusion

Perhaps the best known example of presumptive mimicry between snakes in the New World is to be found among venomous coral snakes and non-venomous mimics (Dunn, 1954; Hecht and Marien, 1956). In coral snakes, the vivid red set off by black, yellow, or white bands has become a classic example of warning coloration with non-venomous mimics coevolving similar color and pattern (for an alternative interpretation, see Greene and Pyburn, 1973). However, the rattlesnake has not evolved any vivid colors or warning coloration but rather is cryptically colored to the human eye. Threat is conveyed most vividly through a warning display (posture and sound). The reluctance of rattlesnakes (Klauber, 1956) to give this warning display until closely approached or

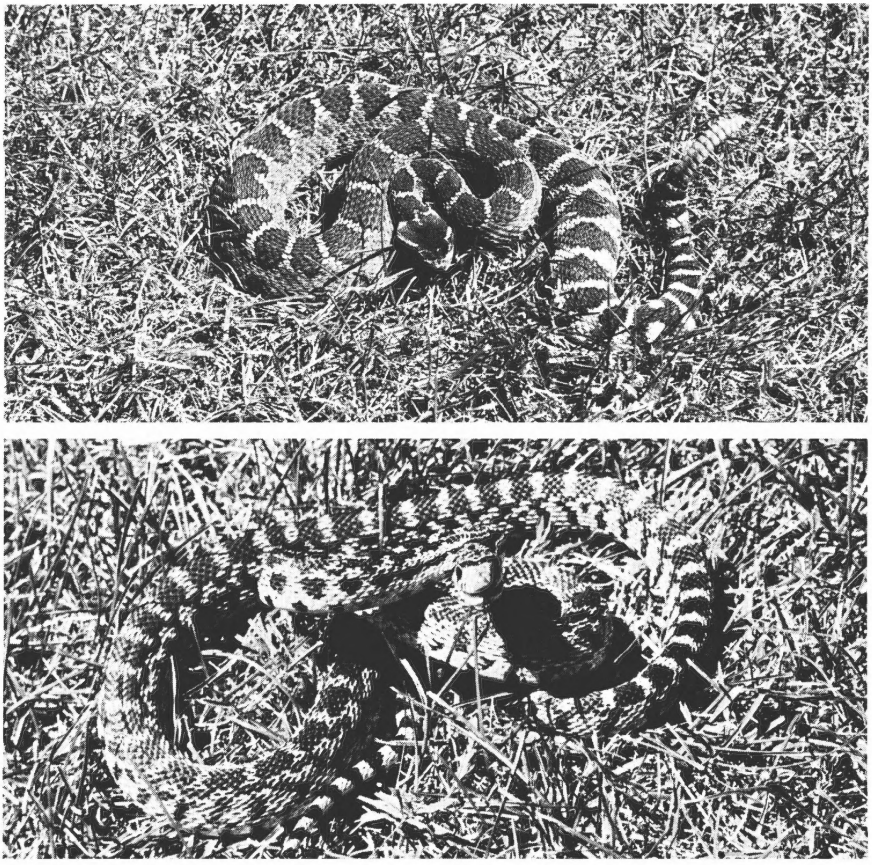

Figure 1. At top, northern pacific rattlesnake (*Crotalus viridis oreganus*) and at bottom, gopher snake (*Pituophis melanoleucus deserticola*). Basic similarity of defensive body posture and dorsal color pattern are shown. The mouth of the gopher snake is slightly parted, allowing air to escape while producing a "hissing" sound.

actually disturbed might be taken as evidence that their defensive strategy is to remain inconspicuous, taking advantage of the camouflage coloration until discovered, whereupon they present a warning display. Examples of this strategy in other species have been proposed (Blest, 1957). Although not vivid, the dorsal blotches of dark color are at least distinctive and could, together with display, become part of the total image presented to a potential predator. If it derived adaptive benefit from confusion with the model, the mimic would be expected to evolve resemblances to the rattlesnake (model) display and color pattern.

Interpreting the rattlesnake and gopher snake as model and mimic respectively in a Batesian mimicry system seems reasonable for several reasons.

First, their geographic ranges closely coincide. Some predators (e.g., birds) move and presumably carry with them disposition to avoid the model so that mimics could evolve outside the range of the model (Hecht and Marien, 1956). However, the fact

that the gopher snake does overlay geographically makes such special hypotheses unnecessary.

Second, the rattlesnake is common and can deliver a highly toxic and painful bite. Frequent encounters with such a formidable prey would strongly reinforce learned predator avoidance and/or be the basis for favoring evolution of innate avoidance (Smith, 1975; 1977). This point would make the rattlesnake a sufficient mimicry model.

Third, both share similarities of color pattern and warning display. Both have dark dorsal blotches set off by intervening light bars or color (Fig. 1). Defensive coiling and even head shape configuration are similar. Although the sound made by gopher snakes is produced by expelling air from the lungs, this sound is easily mistaken for the buzzing sound produced by tail vibration in rattlesnakes.

Fourth, convergence to a similar niche seems an unlikely explanation for the similarities. Though both species are found in the same geographic area, the gopher snake uses a much more extensive part of the habitat (shrubs, trees) and is a faster moving snake than the rattlesnake. These differences in habitat utilization and in locomotor behavior would more likely select for different color patterns more suited to each unique circumstance. This adaptation seems to have occurred in the sympatric yellow-bellied racer (*Coluber constrictor mormon*), which, as an adult, is unblotched and lacks a similar warning display. Finally, it is difficult to imagine what ecological factors would account for the similarities in warning display (posture, tail motion, head shaping, sound production) save for mimicry.

Although this analysis pertains to populations in the northwestern United States, the general similarities between *Pituophis* and *Crotalus* seem to hold throughout their North American ranges (Stebbins, 1966; Wright and Wright, 1957), and Batesian mimicry may be a common coevolutionary feature between these two genera.

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A Comparison of Fish Species above and below Palouse Falls, Palouse River, Washington-Idaho

Abstract

Fish species above and below Palouse Falls did not differ greatly. Exotics above the falls are due to planting. Multiple invasions of cottid species are indicated by exclusion of recent invaders.

Introduction

Natural falls often give insight into the evolutionary history of an area in terms of fish fauna present. Formation of these physical barriers often isolate "ancient" faunal elements and protect them from elimination by more recent invaders. Where isolation is complete and disturbance is minimal, streams above falls can often be used to indicate "primitive conditions" or show relationships between two currently unconnected drainages (Bisson and Bond, 1971; Robins and Miller, 1957). Palouse Falls on the Palouse River isolates fish fauna in upstream areas from those in downstream areas. This characteristic makes the Palouse ideal as a place to look for clues to the faunal history of these mountain drainages.

Description of the Study Area

The Palouse River (Fig. 1) flows from the mountains in northcentral Idaho, through the Palouse Prairie of eastern Washington, and into the Snake River. Near the mouth, the Palouse River plunges 60 m into a large rimrock basin. The river then flows through a canyon before entering Lower Monumental Reservoir on the Snake River.

Methods

Fish were collected from 1968 through 1976 from locations on the Palouse River and tributaries with an AC-DC shocker. Fish were fixed in 10 percent formalin and stored in ethyl alcohol. The depository of the specimens is the Conner Museum, Washington State University, Pullman, Washington, or the museum at the University of Idaho.

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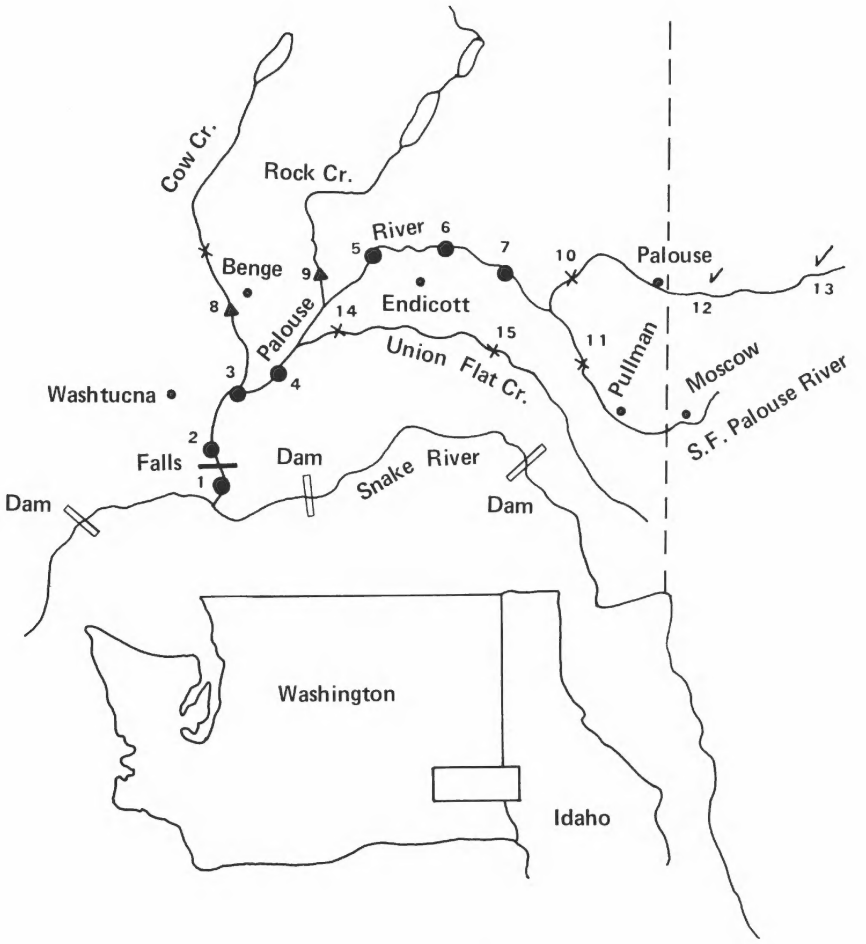

Figure 1. Station locations for collections made on the Palouse River from 1968-1976; △ = stations collected by Maughan, Farris, and Edmundson 1969; ● = stations collected by Maughan, Farris, and Edmundson 1969, and by Wallace 1976; x = stations collected by Wallace 1976 and √ = stations collected by Wallace 1968-1976.

Results and Discussion

Species found above and below the falls did not differ greatly (Table 1). All species taken below the falls except *Cottus beldingi* were also taken at some station above the falls. Excluding exotics, only *Catostomus platyrhnchus*, *Cottus rhotheus*, and *Richardsonius balteatus* were taken exclusively in the upstream sections. Only one specimen of *C. platyrhnchus* was taken.

The species composition of the downstream section was composed of eight native species and three exotics, whereas the upstream collections contained eleven native species and nine exotics. Only exotic species were taken from Cow Creek (Station 8).

TABLE 1. Species list by station above and below Palouse Falls.

Species	Station number and collection year																													
	1		2		3		4		5		6		7		8		9	10	11	12	13	14	15								
	1969	1976	1969	1976	1969	1976	1969	1976	1969	1976	1969	1976	1969	1976	1969	1976	1969	1976	1976	1970	1968-69	1976	1976							
Salmo gairdneri																					x									
Salvelinus fontinalis																					x									
Esox americanus															x	x														
Cyprinus carpio	x	x			x	x					x				x	x	x			x		x								
Acrocheilus alutaceus		x	x	x	x	x	x	x	x	x	x		x	x			x													
Ptychocheilus oregonensis	x	x	x		x	x	x	x	x	x	x		x	x				x	x	x	x	x								
Rhinichthys cataractae	x	x		x				x												x	x									
Rhinichthys osculus	x	x		x		x	x	x	x	x	x	x	x	x				x		x	x	x	x							
Richardsonius balteatus													x								x		x							
Catostomus macrocheilus	x	x			x		x	x		x	x			x			x	x		x	x	x	x							
Catostomus columbianus	x	x		x		x		x			x	x	x					x		x	x	x	x							
Catostomus platyrhynchus					x																									
Ictalurus nebulosus																				x	x									
Cottus rhotheus																					x									
Cottus beldingi	x	x																												
Cottus bairdi		x	x	x			x	x																						
Micropterus dolmieui	x	x													x															
Micropterus salmoides		x															x													
Lepomis microlophus						x			x						x															
Lepomis gibbosus																				x	x									
Pomoxis nigromaculatus			x												x															

Exotics are probably the results of escapes from lakes such as Cow Lake that have been stocked in the past. *R. balteatus* and *C. rhotheus* were taken only above the falls. However, their apparent disrupted distribution is probably the result of sampling error since they are known from other nearby locations below the falls in the Clearwater and Snake Rivers (Maughan, 1976).

The major differences in species composition above and below the falls appeared to be the absence of *C. beldingi* above the falls. *C. beldingi* is the most abundant cottid in the lower Clearwater River and tributaries near the mouth of the Clearwater (Maughan, 1976) and presumably also the lower Snake River. Over much of the Clearwater, *C. rhotheus*, *C. beldingi*, and *C. bairdi* occur sympatrically (Maughan, 1976). Therefore, the absence of *C. beldingi* above the falls probably does not involve competitive exclusion or habitat change.

There is evidence that differences below the species level occur upstream and downstream of the falls. *C. columbianus* above the falls has been designated as a separate subspecies from populations below the falls (Smith, 1966), as has *R. balteatus* above and below the falls (Schultz, 1936). The form of *C. rhotheus* above Palouse Falls does not appear to be the typical *C. rhotheus* described by Smith (1882) and may represent a separate form (Bond, pers. comm.). The form of *C. bairdi* found in the Palouse drainage is not the form described as *C. hubbsi* (Bailey and Dimick, 1949) but is similar to that described as *C. punctulatus*. *C. bairdi* of the *hubbsi* form is the only *bairdi* form found in the Clearwater drainage to the south (Maughan, 1972).

The exclusion of *C. beldingi* and *C. bairdi* of the *hubbsi* form from above the falls would seem to indicate that the Palouse River and its tributaries were subjected to multiple invasions of cottid species and forms from centers of endemism; *C. beldingi* and *C. bairdi* of the *hubbsi* form are more recent invaders than *C. bairdi* ssp. and *C. rhotheus* ssp. Existing populations and distribution resulted from competition, elimination, or integration of these invaders with prior resident species and forms.

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Golden Chinquapin (Chrysolepis chrysophylla) in Washington State: A Species at the Northern Limit of Its Range

Abstract

Golden chinquapin (*Chrysolepis chrysophylla*), an evergreen tree (Fagaceae), reaches its northern limit in Washington as small outlier populations. Some Hood Canal colonies were defoliated by an ascomycetous fungus in 1976 and may not survive. A small colony also occurs at the southeastern edge of the Big Lava Beds, just north of the Columbia River. Small population size, reduced vitality of some individuals, and human activity may adversely affect the fate of the species in Washington.

Introduction

The occurrence of a species at the limits of its natural range has a particular fascination for the evolutionary biologist. Peripheral populations are likely to have different genetic resources and environmental tolerances than those of populations in the heart of the species' range. When such an outlier is a spectacular evergreen tree, the interest in its status is enhanced. The distribution of the golden chinquapin (*Chrysolepis chrysophylla* (Dougl.) Hjelmqvist) is one such case.

Only two small colonies of golden chinquapin are known to occur in Washington: one in Skamania County near the Columbia River and the other 320 km to the northwest in Mason County above Hood Canal. Just south of the Columbia River in northern Oregon, it takes on a more continuous distribution in the Mount Hood area and southward through western Oregon to its southern limit in cismontane northern California.

It is the purpose of this paper to report on the status of the outlier populations of chinquapin in Washington. As a result of the efforts of members of the Washington Native Plant Society and others, a current account of the tree in its few isolated stations can be given.

There are only two species of *Chrysolepis*, both native to western North America. The other species, *C. sempervirens* (Kell.) Hjelmqvist, is a shrub of the mountains of California and southern Oregon. Until 1948, the western North American chinquapins had been retained in *Castanopsis*, a genus now reserved for old world, mainly tropical, species. It was on the basis of features of the bur fruit and the inflorescence that Hjelmqvist (1948) established the genus *Chrysolepis* to embrace our two chinquapin species.

Chrysolepis chrysophylla is an evergreen member of the Fagaceae (Oak Family), of arborescent shrub habit, or a tree to 45 m in height (Figs. 1, 2). It reaches its best growth form as a tree in low elevation, cismontane valleys of northwestern California and southwestern Oregon. At higher elevations or in more xeric habitats, specimens are shrubs, not more than 5-10 m tall. It can occur in a variety of woody plant communities, mostly with conifers like Douglas-fir and coast redwood. Nowhere is it common, and rarely does it occur in pure stands.

Figure 1. Foliage and staminate flowers of *Chrysolepis chrysophylla.* Figure 2. Habit of tree, University of Washington campus. Figure 3. Defoliated tree, Jorsted Creek, Mason County, Washington. Figure 4. Close-up of defoliated branches. (Figures 1 and 2 by W. Marten; figures 3 and 4 by Sigurd Olsen).

For many years the only known locality of golden chinquapin in Washington was along the Columbia River at Moffatt's Spring (now Bonneville Hot Springs, *ca.* 2 km NW of North Bonneville) in Skamania County. The single collection was made in 1904 by M. W. Gorman (cited in Piper, 1906). Attempts by the present author and others to relocate the Bonneville Hot Springs locality have failed. Activities connected with the human settlement of the area and with the construction of Bonneville Dam are likely to have caused its disappearance. Other collections since 1904 have been restricted to the country adjacent to the Big Lava Beds in Skamania County (*ca.* 48 km north of the Gorman locality) and to the disjunct locality west of Hood Canal in Mason County.

The Hood Canal Station

The Washington Environmental Atlas (Anon., 1975) shows three localities in Mason County; near Shelton, at Lake Cushman, and near Eldon. We have confirmed the occurrence of chinquapin in the lower reaches of the drainages of Jorsted Creek and the Hamma Hamma River, both near Eldon. On 19 June 1976, members of the Washington Native Plant Society explored the second growth forest bordering the Jorsted Creek road. Specimens of golden chinquapin were located in section 32 (T24N, R3W3, for about 2 km along Forest Service Road 248A, from Benchmark 998 ft (704.19 m) northwestward. All were nearly completely defoliated, indicating a pathological condition (Figs. 3, 4). I comment on the probable causes and consequence of this defoliation below.

The field party then continued northwest to enter the drainage of the Hamma Hamma River and proceeded east, back down the river road to U.S. Highway 101. About 2 km west of the highway we found a single specimen of chinquapin, a fine tree over 15 m tall, showing no sign of defoliation.

A single specimen was also discovered just off U.S. Highway 101, between the roadway and nearby Hood Canal, 2.5 km south of Jorsted Creek. It is a vigorous, healthy tree, 6 to 8 m tall, with several erect boles from the root crown. One of the trunks had been cut and removed. It is possible that this specimen was transplanted to this private beach property from nearby natural colonies.

In April of 1977, several of us reconnoitered a colony newly discovered by Jim Messmer, a Washington Native Plant Society member. The site is west and within sight of Highway 101. The habitat is a Douglas-fir and hemlock forest on a high bench and adjacent broken terrain, situated about 100 m above the level of the highway. It can be reached by a private road leading west from milepost 322, *ca.* 1.6 km south of Jorsted Creek. This is the largest of the known Hood Canal colonies. Here there are several large trees with boles clear of branches 6-8 m upward to the dense, rounded crowns. Nearby we estimated that there were 150 to 200 smaller trees and saplings back of the high promontory, in open woods (recently thinned by selective logging). On the gravelly slide just below the bench where the largest specimens are growing, there are several bushy chinquapins, presumably seeded there from the mature specimens upslope. The latter produce fruits in fair quantity; beneath the trees we found the spent burs of the previous year's fruit crops.

The finest single specimen of chinquapin in the Puget Sound area is on the north side of Kitsap Lake, just northwest of Bremerton in Kitsap County. It is 60 cm in

diameter with twin trunks, reaching heights of *ca.* 15 m. The tree is on private property near a dwelling. Though its origin and history could not be determined, it most likely was planted by former owners many years ago. The general vicinity is rather densely built up with suburban residences. This single specimen is *ca.* 32 km east of Hood Canal; no intervening colonies have ever been sighted on Kitsap Peninsula. Chinquapins planted on the grounds of private residences have been observed in the vicinity of the Hood Canal natural colonies.

The chinquapins of the Hood Canal area are few in number, occur in isolated colonies, and are in habitats where the forest vegetation is frequently altered by human activity. Moreover, the colonies in the upper Jorsted drainage are undoubtedly severely weakened by the defoliation we witnessed in 1976. The unseasonable loss of leaves is associated with a leaf spot caused by a fungus. Leaves on the ground and the few remaining on the trees all had a dense pattern of black pustules. Thus far the leaf spot symptom appears to be restricted to one colony, though it is only about 5 km west of the healthy grove of chinquapins just above Hood Canal. University of Washington mycologists have tentatively identified the pathogen as a species of *Didymella* (or *Venturia*), an ascomycete.

The Hood Canal stands of chinquapin occur with second-growth Douglas-fir forests of varying age classes and density. The chinquapin appears to be most compatible with Douglas-fir in relatively xeric sites, where the conifer stands are either open or young enough as not to shade the chinquapin. We observed at the milepost 322 site that the best trees were standing in the open, away from Douglas-fir. Also, the recent selective logging had left many spindly saplings of *Chrysolepis* that had evidently been shaded by the 40-60 year old Douglas-fir formerly present. It is our judgment that the fortuitous thinning of conifers at this locality will improve the growth and longevity of the younger chinquapins.

The Big Lava Beds Colony

South central Skamania County, Washington, contains one of the state's most spectacular geologic phenomena: 16,000 acres of land were covered by a Quaternary (450-4000 years B.P.; Hammond *et al.*, 1976) flow of lava leaving a lunar landscape of jumbled, jagged rock, not over 10 m higher (usually only 1-2 m) than the surrounding flat to sloping terrain. Since the flow, the contorted topography of the flow has been thinly colonized by elements of the adjacent flora and by a few exceptional species. A partial checklist of the lava bed's flora is given in the appendix to this paper.

When Don Jole reported in the June 1976 number of *Pacific Search* that he had sighted chinquapin in the Big Lava Beds country, we were anxious to investigate the find. After one failed attempt, in September of 1977 Mareen Kruckeberg and I made a careful search of the southeastern perimeter of the Big Lava Beds, and found several chinquapins in a healthy state. The trees are infrequent and local in flat forested terrain to the south of the lava beds proper. The approximate location of the trees is within section 29 (R9E, T4N); access is along U.S. Forest Service Road N501, *ca.* 2 km west of Forest Service Road N604. The chinquapins here are in both dense Douglas-fir regrowth and in older, more open stands of mixed conifers and hardwoods. The best specimens are in the latter habitat where the forest is composed of Douglas-fir, western hemlock, western white pine, grand fir, western yew, Pacific dogwood, vine maple, and

a rich variety of shrubs and herbaceous species. Individuals are widely spaced in this community, doing best in clearings within the forest. They average 5-15 m in height and tend to have two to several boles per individual. The foliage showed no sign of necrosis or fungal infection. The area is about 40 km north of the Columbia River and the site of the 1904 collection at Bonneville Hot Springs.

Records of the growth of planted chinquapin have been kept at the Wind River Arboretum (Anon., 1959), located about 20 km due west of the Big Lava Beds site. Fourteen trees were planted in 1913, of which ten were surviving in 1956; they had reached a height of 13.8 m,* showing the best growth of any hardwood species in the collection. "The trees (in 1956) are tall and straight, of excellent vigor, and regularly bear fruit. They have produced a large number of natural seedlings throughout the arboretum." A more intensive search in the Wind River drainage is likely to reveal other stands of chinquapin, though none are now around the Wind River Arboretum, nor did we find any along the route from the Big Lava Beds to the Wind River.

State of the Outlier Colonies of Golden Chinquapin

A species at the limits of its range can be expected to have attributes not to be found in the more centrally situated populations. Features likely to differ include vegetative vigor, growth-form (habit), size of populations, reproductive capacity, age-class distribution of individuals, and biotic interactions (pests, competitors, pollinators, dispersal agents, etc.). Further, it would be expected that habitat features such as local climatic regimes, topography, and substrates could differ from outlier status to the center of the range.

Taking the Hood Canal populations as the northernmost native populations of chinquapin, we have found isolated specimens here that match in vigor those in northern Oregon where the tree is more widespread. However, the one grove we relocated on Jorsted Creek is markedly reduced in vigor due to the defoliation, presumably caused by a fungus pathogen. Trees of the Big Lava Bed locality showed no sign of fungal attack and the individuals are as healthy as those in localities where the species is frequent and more continuous in distribution (e.g., the Mt. Hood area of Clackamas County, Oregon).

Golden chinquapin is shade intolerant, at least in the northern sector of its range. It can easily be overtopped in growth by conifers, especially Douglas-fir. As mentioned earlier, the Hood Canal population above milepost 322 (U.S. Highway 101) showed the effects of conifer shading. Saplings and small trees of chinquapin that were closely surrounded by Douglas-fir and western hemlock were spindly and leafless nearly to their tips. Selective logging of the site may improve the chances of survival of these trees. On a nearby open promontory, the chinquapins have sturdy boles and ample, leafy crowns. Following fire and/or logging, golden chinquapin can compete well for a time with the conifer regrowth. But given the more rapid growth rate of the conifers, the chinquapin is sure to become suppressed in growth beneath the canopy of dominant needle-leaved evergreens. This adverse response of an evergreen hardwood to shading has also been noted in the case of *Arctostaphylos columbiana* (Kruckeberg, 1977).

Reproduction of chinquapin has been commented on by several authors (Douglas,

*Douglas-fir can be expected to grow 25.6 m tall in the same length of time.

1826; Jepson, 1910, Schopmeyer, 1974, Vandersal, 1939). It is said to fruit sparingly, and to set few seed with low germinability (14-59 percent). Seed stored at 41°F can remain viable up to five years (Schopmeyer, 1974). None of the authors comment on the occurrence of seedlings in the California and Oregon populations. We have not discovered seedlings or small saplings in the native groves of Washington, unlike the abundant reproduction of plantings at the Wind River Arboretum. It is not known if golden chinquapin, a monoecious species, is self-compatible. If it were, and if seed from selfed parents were less vigorous, then single isolated trees or small groves might have a lowered reproductive output.

Natural vegetative propagation by layering or suckering may possibly occur. Sucker growth could account for the clump or thicket-forming nature of certain specimens. Intentional coppicing to induce sucker growth has not been reported. Neither is it known if golden chinquapin can crown-sprout after fire. We must conclude, therefore, that the reproductive capacity of chinquapin is low and that the prospects for maintaining even small populations at the periphery of the range are not good. In the absence of natural or man-made disturbance, the isolated stands of chinquapin in Washington may not persist indefinitely.

Although such human activities as clearcut logging, burning, land development, etc. probably would eliminate the Washington colonies, other kinds of human interference in chinquapin habitats may be beneficial. Selective logging or pre-commercial thinning of associated conifers and deciduous hardwoods (maple, alder, and cottonwood) prevent suppression of the slower growing chinquapin, and provide a suitable seed bed and nursery for chinquapin progeny. The Washington Native Plant Society will encourage custodians of forest land to manage chinquapin habitats in Washington so as to preserve the existing trees and to foster their reproduction.

Our field studies of golden chinquapin might be expected to give some clues as to the causes for both the isolated Washington colonies and for the northward termination of the species' range. Yet some of the small isolated populations seem just as healthy as those in the core portions of the species' range, while one population appears in danger of extinction; size of population, then, is not the limiting factor.

Physical factors in the environment are not perceptibly different between northern Oregon and the outlier habitats in west central Washington. Regional climates from the Columbia River and northern Oregon to Puget Sound are not appreciably different, especially when one considers local climatic regimes, some of which would closely match those in chinquapin habitats further south. It is possible that occasional occurrences of extremes in climate could limit the ability of the peripheral isolates to persist or to expand their ranges northward. Mason (1936) has argued for this interpretation, using the example of coast redwood and the growth-deterring conditions of an extreme year (1932). Perhaps we are obliged to resort to the suitably vague biogeographic law that species are limited in their distributions by limits in their physiological tolerance to environmental factors (Cain, 1944). But we are still left to wonder which particular set of environmental attributes (and at what intensities) is operating to determine the limits to distribution.

Unique and even capricious episodes of dispersal no doubt have placed outliers of a species well beyond its usual range. Two modern authors (Brockman, 1958; Scheffer, 1961) have seized upon one such explanation, first hinted at by David Douglas in 1826.

Douglas found chinquapin seeds in the crop of a band-tailed pigeon he had shot some 320 km from the nearest source of the tree. Could the Washington plants have come from such a chance dispersal? The same explanation has been invoked to account for the very local occurrence of *Pinus pondersoa* on the Fort Lewis prairies, the only location of ponderosa pine west of the Cascades in Washington.

If the geologist's aphorism is reversed to read "the past is a key to the present," we are led to a paleoecological basis for present chinquapin distribution. Wolfe (1969) lists chinquapin as one of many woody plants that were present in the early and middle Miocene flora of the Pacific Northwest. Not only did it persist through the Pleistocene, but Wolf suggests that it could have evolved from a summer-wet Mixed Mesophyte forest species to become adapted to the more xeric summer-dry conditions of the post-Pleistocene, especially during the warm (Hypsithermal) interval between 5000 and 3000 years B.P. In this view, chinquapin may be interpreted as a relictual species at present, persisting locally from a time when it could have been both more continuous and further north in its distribution.

Appendix

Partial list of the plants of the Big Lava Beds, Skamania County, Washington.

Trees
- Abies lasiocarpa (northern sector)
- Pseudotsuga menziesii
- Pinus contorta
- P. monticola

Shrubs
- Acer circinatum
- Arctostaphylos columbiana
- A. nevadensis
- Garrya fremontii
- Holodiscus discolor
- Juniperus communis
- Pachystima myrsinites
- Rhamnus purshiana
- Vaccinium parvifolium

Herbs
- Apocynum androsaemifolium
- Cheilanthes gracillima
- Comandra umbellata
- Cryptogramma crispa
- Goodyera oblongifolia
- Penstemon fruticosus
- P. rupicola
- Polystichum munitum
- Xerophyllum tenax
- Woodsia oregana

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Phenological Relationships of Spiraea betulifolia Pall. and Apocynum androsaemifolium L.

Abstract

The phenology of two widespread understory species was examined at three elevations during two seasons, 1972 and 1973. Occurrence of several identified phenological phases related well to the accumulated temperature at the site but poorly to calendar date or soil moisture content. Phenological phases of transplant stock from high to low elevation and the reverse followed native plants at the site in the case of *Spiraea*, but were seemingly insensitive to local control in the high to low transplants of *Apocynum*.

Introduction

Forest and range sites, especially in the mountainous terrain of western North America, can range in local climate from desert to alpine within short distances. Climatic measurements at all locations would be difficult. A chronology of the stages of native plant development (phenological phase) may be helpful in comparing climatic regimes and their seasonal progression, especially at harsh sites. Such a chronology should lead eventually to a more informed selection of management techniques.

The main requirements for precision in site evaluation by this method are the sensitivity of the phenological phase to climate and the ability to determine some presumably causal relationship between phenological phase and the climatic factors. Although some phases of plant development may be controlled by a single factor, the plant in general responds to a composite of external and internal controls. Due to simplicity and to past successes, a thermal index is often used in describing the phenological relationship. Wang (1960, 1972) presents an interesting historical account of development of phenological observations and the thermal index and evaluates performance of this approach.

To determine the utility of phenology in evaluating climate at remote forest sites, the relationship between phenological phase of two common understory plant species and thermal and soil moisture regimes at three elevations was examined. The elevations selected encompass the major portion of the elevational range of distribution of the two species.

Methods

Spiraea betulifolia Pall. (birchleaf spirea) and *Apocynum androsaemifolium* L. (spreading dogbane) were selected for evaluation in this study. *Spiraea* is a rhizomatous shrub

found from British Columbia southward to north central Oregon. *Apocynum* is a perennial herb that develops from strong rhizomes. Distribution is throughout much of Canada and most of the U.S. except the southeast (Hitchcock and Cronquist, 1973). In north central Washington both plants are common components of the understory of *Pinus ponderosa* Laws, and *Pseudotsuga menziesii* (Mirb.) Franco. *Spiraea* also occurs locally within *Abies grandis* (Dougl.) Lindl. and *Abies lasiocarpa* (Hook.) Nutt. associations into northern Idaho (Franklin and Dyrness, 1973).

Four groups of plants (consisting of three to eight individuals) of each species (sometimes intermixed) were selected at three sites on the Entiat Experimental Forest (lat. 47° 57′ N, long. 120° 28′ W) at elevations of 590 m, 1105 m, and 1635 m. All sites were within 3.2 km horizontal distance. The highest elevation site was near the elevational limit for both species in this locality. Aspect is southerly to southwesterly, and direct solar radiation is normally available from mid-morning into the early evening hours.

Eastern Washington is an area of winter precipitation maxima; snow is common at these sites with overwinter accumulations varying from 1-2 m in depth. Summer precipitation is infrequent, occurring as showers and thunderstorms.

Shoots of all *Spiraea* plants in 1972 were two years old or less; wildfire destroyed above-ground parts of all plants in August 1970. *Spiraea* varied in height from about 60 cm at the lower site to less than 30 cm at the higher site. *Apocynum* varied from near 75 cm maximum height at the lower site to about 30 cm at the upper site. Plants were vigorous and well formed at both lower and middle sites. At the upper site, plants were stunted and possibly still recovering from the fire damage. Phenological phases that were selected on the basis of prior observation of these species are shown in Table 1.

Phenological phase was observed during the spring to fall of 1972 and 1973. Initial observations were made as soon as access to the sites was possible and on an average at weekly intervals throughout the growing season. Average dates for plants to reach each stage were assembled by site for the analyses.

TABLE 1. Average and range of temperature integral and relative accuracy of phenological phases.

	Phenological phase	Degree hours ($x10^3$) Average	Range	Relative accuracy[1]
Spiraea	Bud break	0.8	0.1-2.2	2
	4-6 leaf	2.2	1.2-3.6	3
	Floral initiation	8.0	6.5-11.4	4
	First bloom	17.1	15.0-19.0	1
	Peak bloom	22.3	19.8-24.2	5
Apocynum	Emergence	4.3	3.0-5.8	4
	Floral initiation	12.7	11.0-14.4	3
	First bloom	18.2	17.0-20.6	1
	Peak bloom	25.6	23.2-28.0	2

[1]Accuracy = occurrence of a specified phase for all plants at a site. 1 = highest, i.e., least variation in time for phase occurrence. 5 = lowest, i.e., greatest variation in time for phase occurrence.

The estimates of relative accuracy shown in Table 1 indicate our ability to detect exact timing for each phase. Entry into a given phenological phase varied from several days up to as much as two weeks among individual plants at any site. Of the pheno-

logical phases selected for observation in this study, first bloom was the most accurately determinable phase for both species (Table 1). After bloom had commenced on *Spiraea*, floral initiation continued as long as dwindling soil moisture reserves allowed vegetative growth. Some inflorescences might be past peak bloom on a branch with immature florets. Emergence of *Apocynum* sprouts was the least accurately determined phase for this species, although sharper than the peak bloom of *Spiraea.*

For our temperature index, a continuous linear electrical analogue of all temperature excursions above a base temperature 0° C was digitized and accumulated. Temperature accumulation was in counts per hour equal to degree hours.

Night as well as day temperature was included in the degree hour summary. The continuous accumulation method automatically determines the actual area under the temperature curve and avoids any assumption about the shape of the diurnal temperature curve. The temperature sensor was shielded from the sun by a 6-cm diameter aluminized mylar-covered, styrofoam sunshield. Sensor and shield were mounted on a flexible plastic rod with the sensor at 0.5 m above the ground surface. Sensor height at 0.5 m was more representative of the microclimate of the low shrub and herb than a sensor installed at standard weather shelter height. The cumulative temperature integral was read each time the site was visited and was used as the ordinate ("Y" axis) in Figures 1 and 2.

A number of alternatives exist for the generation of a thermal index. Base temperatures, method of summation, or combinations with other variables (*e.g.*, solar radiation)

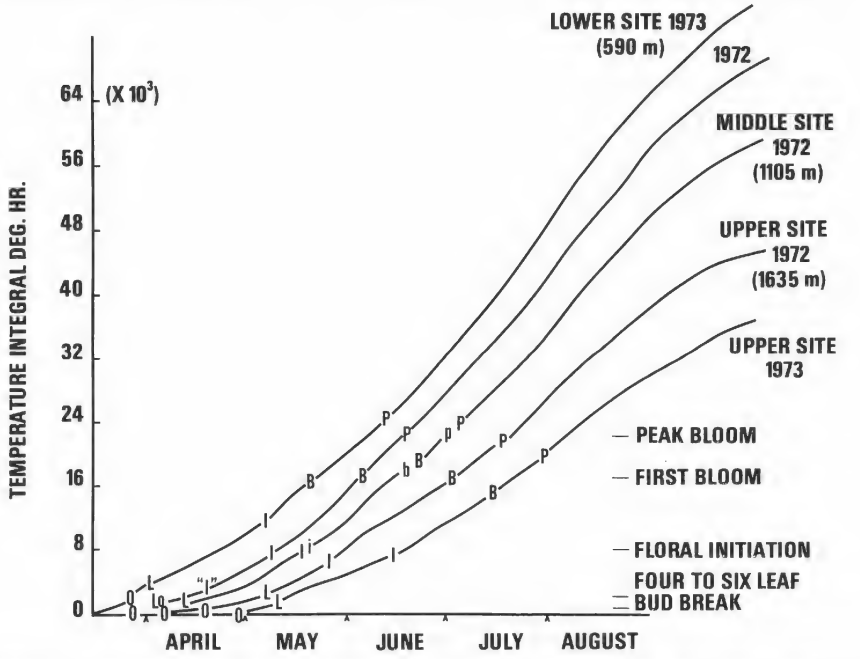

Figure 1. Temperature integral and phenological phases of *Spiraea.* Lower case letters represent 1973 data from middle elevation site. "I" represents 1973 floral initials destroyed later by frost.

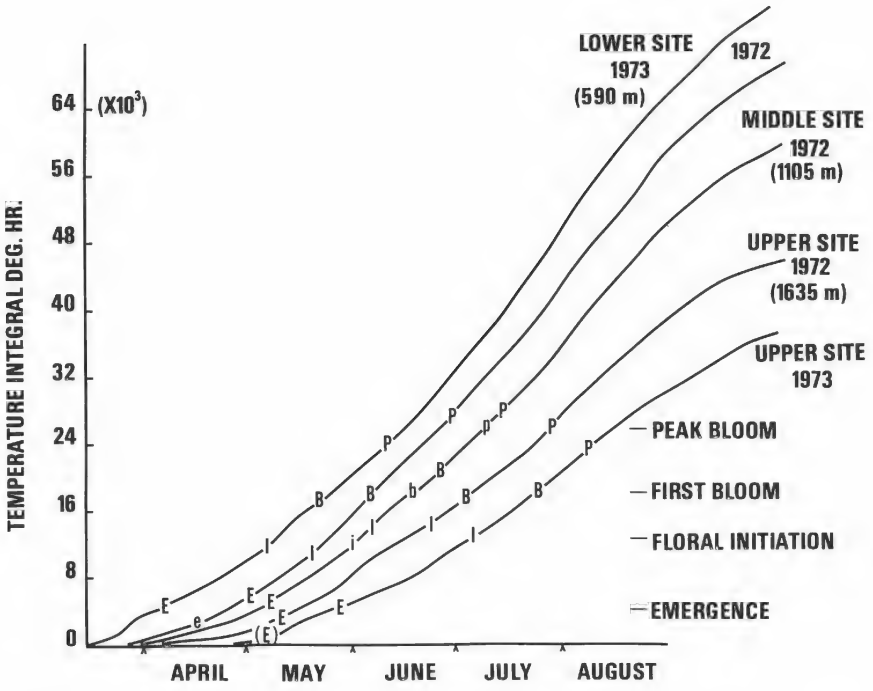

Figure 2. Temperature integral and phenological phase of *Apocynum*. Lower case letters represent 1973 dates from middle elevation site. (E) represents 1973 emergence, plants later destroyed by frost.

have been utilized (Caprio, 1971). Recently Sauer (1976) described a "moving averages" procedure found to be more descriptive in his application than the cumulative sum of temperatures. The simple linear accumulation was for us the most appropriate, given instrumental constraints.

Soil moisture content (gravimetric, percent of dry weight) was monitored at depths 0 to 15 cm and 15 to 30 cm throughout the summer of 1973.

An additional test to evaluate ecotypic variation between plants at upper and lower elevational sites was initiated in late fall of 1972. This test involved transplanting dormant *Spiraea* and *Apocynum* from low to high elevation sites and the reverse.

Results and Discussion

Average dates of phenological phases for *Spiraea* (Fig. 1) and for *Apocynum* (Fig. 2) are compared to the accumulated temperature integral for lower, middle, and upper elevation sites for 1972 and for lower and upper elevations in 1973. Vandalism and subsequent instrument failure invalidated direct measurement of temperature integral for middle elevation sites in 1973. Data for the middle elevation site in 1973 were generated from regressions developed from 1972 data. Correlation coefficient (1972) between temperature integrals at sites was: middle to upper + lower, $r = .9992$; middle to lower, $r = .9973$. The computed middle elevation curve for 1973 fell along the 1973

curve shown for the lower elevation site and overlapped the 1972 plot for the middle elevation in early May. To avoid confusion, only the temperature integral for 1972 at the middle elevation site is shown. The general trend of the temperature integral indicates that 1973 at the lower site was generally warmer while the higher site was cooler.

Horizontal alignment of the letters representing the several phenological phases for *Spiraea* (Fig. 1) indicates that a similar temperature integral at each site was reached corresponding to each phenological phase. In a comparison of 1972 to 1973, timing differed at the upper and lower sites by about three to four weeks but by only a week or less at the middle site. Over the range of sites on the watershed complex, time differences were as long as two months in these two years. First bloom, for example, at the lower elevation site occurred mid-May in 1973 compared to mid-July in 1973 at the upper elevation site. Average and range of the temperature integral for the phenological phases of *Spiraea* are shown in Table 1. Largest departures from the average are in the 1973 data from the lower site and the peak bloom data at the upper site.

The occurrence of early spring in 1973 at the lower site is shown by the rapid increase of the temperature integral in late March (Fig. 1). A reduced temperature integral occurred in early April accompanied by heavy frost which killed most of the early growth. Timing of *Spiraea* floral initiation was retarded as new shoots were produced. First bloom at this site, however, was at about the average temperature integral for plants at these sites.

At the upper site in 1972, phenological phases for *Spiraea* were close to the average temperature integral. Seeds formed on all plants. During 1973, the temperature integral was retarded at the upper site compared to 1972. Blossoming and seed production were generally poor. Within the total of all sample plants at the upper site, one failed to bloom, the rest had only a sparse bloom, and no seed was formed. The timing shown for first bloom and peak bloom at this site for 1973 represented only the most precocious plants; it is biased in the direction of an earlier date and a consequently lower temperature integral.

Average and range of temperature integral for *Apocynum* is also shown in Table 1. Alignment of phenological phase at the elevational sites (Fig. 2) is again near the average values. Two dates for emergence are noted at the upper site for 1973: frost destroyed the initial group of plants, and for the second flush, emergence coincided with the average temperature integral, but conditions were below marginal limits for seed production. In 1972 all plants produced flowers but no seeds were produced. In 1973 one group of plants did not develop floral initials, one-quarter to one-half of the total plants did not bloom, and no seed pods were produced on any plants at the site.

Response of transplanted stock, compared to natives at a site, was mixed. Bud break and four- to six-leaf stage of *Spiraea* transplants (upper site to lower site) were somewhat retarded (one week) at the lower site but advanced by about a week at the upper site. Although high to low transplants showed floral initiation about the same time as natives, first bloom was delayed by 10 to 15 days. Peak bloom, floral initiation at both sites, and first bloom at the upper sites were essentially the same for transplant and local groups.

Apocynum transplants from the upper site to lower site were retarded in phase up to a month behind natives at the lower site. Lower transplants were somewhat advanced (one week) in first bloom and peak bloom at the upper site.

Transplants of both species failed to produce seeds at the lower site. Foliar yellowing and drying occurred a month earlier on *Spiraea* and two weeks earlier on *Apocynum* than natives at the lower site. Lower to upper transplants of both species flowered and developed seeds. Inflorescences of *Spiraea* and seed pods of *Apocynum* were smaller, by as much as 50 percent, than plants at the lower site.

Soil moisture at depth 0 to 15 cm and 15 to 30 cm (average of two samples per depth) is shown (Fig. 3) for 1973 sample dates. Site variability and a July rain shower account for the irregular shape of the curve. The moisture content declines as the season progresses until the early fall rains in September. Phenological phases for both *Spiraea* and *Apocynum* are also shown at the three sites.

Although most roots of these plants are found in the 0- to 30-cm depth, little correlation between soil moisture-phenological phase is evident. No correlation exists between the 15- to 30-cm moisture contents and phenological phase for either species. Soil moisture at 15 to 30 cm at the upper site never declined to the initial values for 15 to 30 cm at the lower site. First bloom and peak bloom of *Spiraea* did occur with 0- to 15-cm moisture contents of about 3 to 5 percent at each site. Similarly, first bloom and peak bloom of *Apocynum* occurred with moisture contents in the 0- to 15-cm layer of about 3 to 5 percent.

Conclusion

Phenological phases of *Spiraea* and *Apocynum* are intimately related to the site's thermal regime. Phenological phases occurred near an average temperature integral for the two

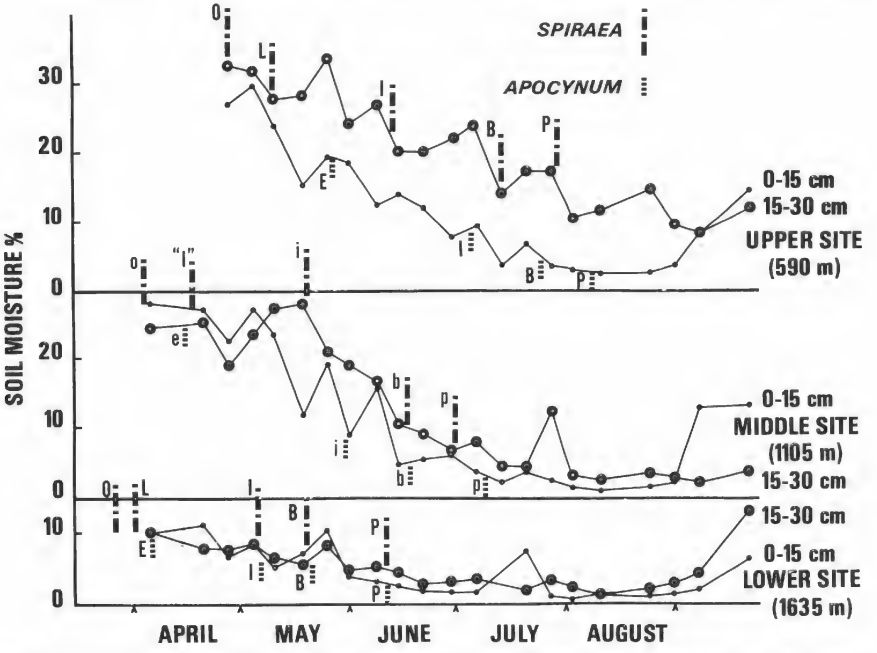

Figure 3. Trends of soil moisture at two depths and phenological phase of *Spiraea* and *Apocynum*. Letter symbols are as shown in Figures 1 and 2.

years examined, even though in 1973 at the lower site temperatures were noticeably above the 1972 values while at the upper site they lagged behind 1972 values considerably. Departures from the average are believed to depend on:

(1) accuracy of the observation of phase; i.e., whether all plants at the site enter a phase simultaneously;
(2) the variable effects of frost on active plants, the survivors of the event, and replacements; and
(3) observational error or inadequate specification of phenological phase or local temperature integral.

Certain phases of development of these species, bud break, first bloom, and emergence, offered less opportunity for observational bias. Peak bloom on *Spiraea* and floral initiation on both species offered a greater opportunity for bias and inaccuracy among observers (four observers during the two years), since these phases were relatively ill-defined.

In the life zone occupied by these plants in the field, small differences in soil moisture and other soil physical properties, shading, radiative exchange, air drainage in the irregular ground surfaces, and mutual protection created a range of micro differences in the total climate. Our single temperature measurement per site reflected only a sample of this diversity, although attention was given initially to selection of relatively similar plant groupings at locations near the sensor.

At the time when the lower site temperature sensor was being installed, snowmelt at most favored locations had eliminated the snow cover, although up to 0.5 m of snow remained only meters away. Plants at these favored locations were responding to their unique thermal regime. *Spiraea* into the four- to six-leaf stage could be found, although the main plant community had not emerged from beneath the snow pack.

Temperature measurements were started as soon as access permitted. Any temperature excursions above the 0° C base experienced at sites prior to this time were unobserved. To have had *Apocynum* emergence at the upper site in early May 1973 indicates soil became bare early; air and soil temperatures necessarily were above 0° C and therefore an unknown quantity was not accounted for in determination of the temperature integral for this site. Addition of this quantity would have strengthened the temperature integral-phase relationship for all plants at this site.

Provenance and its relationship to phenology has come under investigation. Campbell and Sugano (1975), for example, found strong correlations between timeliness of bud break and provenance of Douglas-fir. Our attempts to test the elevational differences in *Spiraea* and *Apocynum* were unfortunately confounded by transplant shock, inadequate time for establishment (especially at the lower elevations), and the poor vigor of transplant stock. This question remains unresolved for plants moved to lower elevations. Phenological phases of plants brought to the upper elevation generally occurred within a week or less of native plants of both species. *Apocynum* transplants at the lower site were notably "off cycle" compared to natives. With emergence tied directly to soil temperature (no plant parts were exposed above ground), variation in planting depth could have seriously affected the plant response.

Seasonal progression of plant phases did not relate well to calendar date or to an apparent photoperiodic control. Advances or lags of up to three weeks for the date of a phase were found at the lower and upper site with less than a week's phase shift at the

middle site. By contrast, Heinrich (1976) found native *Spiraea* (*S. latifolia, S. tomentosa*) along with most plants in his study area (a Maine bog), with little year-to-year variation in their flowering times. *S. latifolia* varied about a week in flowering times during 1972, 1973, and 1974. "The differences in flowering times, particularly of the bog plants (natives), appear to be small in view of the marked differences in weather over the five years."

There appears to be only a weak relationship between phenological phase of these species and soil moisture content at 0 to 15 cm and none to moisture content at 15 to 30 cm. The utility of a proven relationship of this type would be of great value during rehabilitation efforts on harsh sites where success of planting could relate directly to available soil moisture.

As defined initially, we sought relationships that could be used to classify sites as to their general climates and seasonal differences. With the average values established for the various phenological phases, this classification is possible at sites within the range of these species. Timeliness of achieving a phenological phase at a site may indicate for this plant and others the likelihood of completion of its annual cycle. Sensitive forage plants might well be excluded from grazing, for instance, if completion of an annual cycle is not expected. If either *Spiraea* or *Apocynum* were to be protected, early recognition in 1973 that seed production was marginal would signal restriction of consumptive use. Community stability depends on the continued success of reproduction of desired species.

Spiraea and *Apocynum* appear to be satisfactory indicator plants for climatic conditions at these sites. Broadening this type of study to other sites would strengthen the relationship developed here. The temperature integral as defined electrically in this study appears to be a suitable method to accumulate necessary climatic data. Efforts to include other factors which directly influence herb emergence and inclusion of other species could be fruitful research. Soil temperature, for example, is an important factor to consider.

Even though the phenological relationship of these plants was found to be best for first bloom, encouragement should be given to observation of the several phases of the plant for a seasonal characterization of the local climatic regime.

In a number of studies and a variety of species of plants, progression of flowering times have been related to latitude and altitude. Long-term averages of flowering time appear to group near four days/1° latitude and four days/100 m in elevation. With the middle site as a reference, averages of the 1972-1973 seasons indicate about a ± 20-day departure of phenological phase for the ± 500 m altitude difference or near the four days/ 100 m values. Recognition and utilization of the year-to-year variation about this average is implied to be the more significant tool in site management.

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Mites (Excluding Chiggers) from the Fur of Five Species of Western Oregon Shrews[2]

Abstract

The more abundant mites from 685 shrews of five species from Oregon were: *Protomyobia brevisetosa, Amorphacarus* n. sp., *Orycteroxenus soricis, Euryparasitus* sp., and *Hirstionyssus obsoletus* (var.) from the marsh shrew (*Sorex bendirii*); *P. brevisetosa, O. soricis, Euryparasitus* sp., *H. obsoletus* (var.), and *Amorphacarus hengererorum* from the Pacific shrew (*S. pacificus*); *O. soricis, Haemogamasus occidentalis, Euryparasitus* sp., and *P. brevisetosa* from the Trowbridge shrew (*S. trowbridgii*); *P. brevisetosa, Androlaelaps fahrenholzi, A. hengererorum, Euryparasitus* sp., and *H. occidentalis* from the Wandering shrew (*S. vagrans*); and *H. obsoletus* (var.), *A. hengererorum, P. brevisetosa, O. soricis*, and *H. occidentalis* from the Yaquina shrew (*S. yaquinae*). A new species of *Amorphacarus* was found on *Sorex bendirii* and is currently being described. Mites here reported for the first time from Oregon are *Amorphacarus hengererorum, Orycteroxenus soricis, Eucheyletia bishoppi*, and *Pygmephorus designatus*. Nearly all parasites found during this work constitute new host records.

Introduction

There are no data on mites found in the fur of either *Sorex bendirii* or *S. yaquinae*, and there is relatively little information on mites from other species of western shrews (Whitaker and Wilson, 1974). The only paper specifically on mites of Oregon mammals is by Hansen (1964), although Herrin (1970) included a number of state records for *Hirstionyssus*. The purpose of this paper is to present information on mites (excluding chiggers) found in the fur of five species of shrews of Oregon.

Methods and Materials

Shrews examined during this study were taken mostly in unbaited snap traps. Ectoparasites and other organisms were collected by brushing the hosts over a white porcelain pan with a finely bristled toothbrush. Hosts were then examined by blowing their fur and picking off additional mites. Parasites were preserved in a 70 percent ethanol,

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stained in Nesbitt's solution containing acid fuchsin, and mounted in Hoyer's solution. Cover slips were ringed with Euparal.

The study area has been described by Whitaker and Maser (1976). Shrew nomenclature follows Jackson (1928) and Johnson and Ostenson (1959).

Results and Discussion

Numbers and species of mites found on five species of shrews (*Sorex bendirii, S. pacificus, S. trowbridgii, S. vagrans,* and *S. yaquinae*) are given in Table 1.

The most abundant mites listed in decreasing order of abundance for each species were: *Protomyobia brevisetosa, Amorphacarus* n. sp., *Orycteroxenus soricis, Euryparasitus* sp., and *Hirstionyssus obsoletus* (var.) from *Sorex bendirii*; *P. brevisetosa, O. soricis, Euryparasitus* sp., *H. obsoletus* (var.), and *Amorphacarus hengererorum* from *Sorex pacificus*; *O. soricis, Haemogamasus occidentalis, Euryparasitus* sp., and *P. brevisetosa* from *Sorex trowbridgii*; *P. brevisetosa, Androlaelaps fahrenholzi, A. hengererorum, Euryparasitus* sp., and *H. occidentalis* from *Sorex vagrans*; *and H. obsoletus* (var.), *A. hengererorum, P. brevisetosa, O. soricis,* and *H. occidentalis* from *Sorex yaquinae.*

Three laelapids (*Haemogamasus occidentalis, Androlaelaps fahrenholzi,* and *Hirstionyssus obsoletus*), and one myobiid (*Protomyobia brevisetosa*) were found on all species of hosts. The cyrtolaelapids (*Euryparasitus* spp.) were also recovered from all species of shrews, but more than one species is involved. Two species of mites (*Orycteroxenus soricis* and *Haemogamasus reidi* were found on four of the host species.

Among the laelapid mites, *H. occidentalis* is a common large mite on many western mammals, and *A. fahrenholzi* is common on many North American hosts (Whitaker and Wilson, 1974). *Haemogamasus reidi* is found on a number of hosts, especially squirrels. *Hirstionyssus obsoletus,* the most abundant mite on *Sorex yaquinae,* was taken on all five species, and was among the most abundant mites on three species. It varied from typical *obsoletus* in having the ventral spine on coxa II acute; this form is under further study.

Myobiid mites are often common on shrews. Three species in this family were found in Oregon. *Protomyobia brevisetosa,* found on all five host species, was the most abundant mite on *Sorex bendirii, S. pacificus,* and *S. vagrans. Sorex trowbridgii* was notable in having only one myobiid species present, and in having a very low rate (1 percent of shrews infested, 0.02/host) of infestation (Table 1). The other four shrews each harbored a species of *Amorphacarus, A. hengererorum* on *Sorex pacificus, S. vagrans,* and *S. yaquinae,* and a new species of *Amorphacarus* on *Sorex bendirii.* The new species is currently being described (Fain and Whitaker, 1978).

Orycteroxenus soricis is the major glycyphagid of many North American shrews and was common in our sample. The numbers in Table 1, however, represent only the mites actually preserved. The posterior clasping organs, which allow this species to cling to individual hairs, make it difficult to collect by brushing, and it undoubtedly was much more abundant than the table indicates.

One other mite deserving special mention is *Euryparasitus* sp. We have often found *Euryparasitus* nymphs on small mammals, but the numbers found during this study were much higher than usual. More than one species of *Euryparasitus* was involved, but the relationship between host and mite is not known.

TABLE 1. Mites from shrews from Oregon.

	Sorex bendirii n = 33		Sorex pacificus n = 59		Sorex trowbridgii n = 392		Sorex vagrans n = 37		Sorex yaquinae n = 164	
	Total No. parasites (No./host)	No. infested (%)	Total No. parasites (No./host)	No. infested (%)	Total No. parasites (No./host)	No. infested (%)	Total No. parasites (No./host)	No. infested (%)	Total No. parasites (No./host)	No. infested (%)
MOSTLY PARASITIC OR PHORETIC FORMS										
Laelapidae										
Hirstionyssus obsoletus (var.)	15 (0.45)	6 (18.2)	24 (0.4)	5 (8.5)	6 (0.02)	6 (1.5)	1 (0.03)	1 (2.7)	52 (0.3)	6 (3.7)
Haemogamasus occidentalis	6 (0.18)	6 (18.2)	6 (0.1)	6 (10.2)	151 (0.4)	102 (26.0)	7 (0.2)	4 (10.8)	12 (0.07)	8 (4.9)
H. reidi	5 (0.15)	4 (12.1)	—	—	2 (0.01)	2 (0.5)	1 (0.03)	1 (2.7)	1 (0.01)	1 (0.6)
H. ambulans	—	—	—	—	—	—	—	—	1 (0.01)	1 (0.6)
Androlaelaps fahrenholzi	1 (0.03)	1 (3.0)	2 (0.03)	1 (1.7)	5 (0.01)	4 (1.0)	10 (0.3)	2 (5.4)	1 (0.01)	1 (0.6)
A. casalis	—	—	—	—	1 (0.003)	1 (0.3)	—	—	—	—
Eulaelaps stabularis	—	—	—	—	4 (0.01)	4 (1.0)	1 (0.03)	1 (2.7)	—	—
Eubrachylaelaps debilis	—	—	—	—	2 (0.01)	2 (0.5)	—	—	—	—
Alphalaelaps aplodontiae	—	—	—	—	1 (0.003)	1 (0.3)	1 (0.03)	1 (2.7)	—	—
Laelaps alaskensis	—	—	9 (0.2)	2 (3.4)	—	—	1 (0.03)	1 (2.7)	—	—
Myobiidae										
Protomyobia brevisetosa	72 (2.18)	11 (33.3)	109 (1.8)	16 (27.1)	9 (0.02)	4 (1.0)	12 (0.3)	1 (2.7)	30 (0.2)	9 (5.5)
Amorphacarus n. sp.	36 (1.08)	4 (12.1)	—	—	—	—	—	—	—	—
A. hengererorum	—	—	19 (0.3)	6 (10.2)	—	—	8 (0.2)	3 (8.1)	32 (0.2)	10 (6.1)
Glycyphagidae										
Orycteroxenus soricis	21 (0.64)	2 (6.1)	24 (0.4)	5 (8.5)	170 (0.4)	67 (17.1)	—	—	28 (0.2)	8 (4.9)
Glycyphagus hypudaei	4 (0.12)	1 (3.0)	1 (0.02)	1 (1.7)	1 (0.003)	1 (0.3)	—	—	—	—
Listrophoridae										
Listrophorus mexicanus	1 (0.03)	1 (3.0)	—	—	—	—	—	—	—	—
Cheyletidae										
Eucheyletia bishoppi	—	—	1 (0.02)	1 (1.7)	3 (0.01)	3 (0.8)	—	—	—	—
Pygmephoridae										
Pygmephorus horridus	—	—	—	—	3 (0.01)	3 (0.8)	—	—	1 (0.01)	1 (0.6)
P. designatus	—	—	—	—	1 (0.003)	1 (0.3)	—	—	—	—
Pygmephorus sp.	—	—	1 (0.02)	1 (1.7)	4 (0.01)	3 (0.8)	—	—	—	—
Bakerdania sp.	—	—	—	—	4 (0.01)	3 (0.8)	—	—	1 (0.01)	1 (0.6)
OTHER FORMS										
Cyrtolaepidae										
Euryparasitus sp.	18 (0.54)	13 (39.4)	22 (0.4)	14 (23.7)	66 (0.2)	57 (14.5)	8 (0.2)	3 (8.1)	8 (0.05)	5 (3.0)
Cyrtolaelaps sp.	—	—	—	—	2 (0.01)	2 (0.5)	1 (0.03)	1 (2.7)	—	—
Miscellaneous mites										
Pseudoparasitus sp.	—	—	—	—	1 (0.003)	1 (0.3)	—	—	—	—
Anoetidae	1 (0.03)	1 (3.0)	1 (0.02)	1 (1.7)	4 (0.01)	1 (0.3)	—	—	—	—
Proctolaelaps sp.	—	—	—	—	3 (0.01)	3 (0.8)	—	—	—	—

Mites not previously reported from Oregon, other than the new species, are *Amorphacarus hengererorum*, *Orycteroxenus soricis*, *Eucheyletia bishoppi*, and *Pygmephorus designatus*.

There are no previous records of mites from *Sorex bendirii* or *S. yaquinae*; thus all mites reported are new host records. *Protomyobia brevisetosa* had previously been reported from *Sorex pacificus* by Jameson and Dusbabek (1971). The remaining records from that species constitute new host records. *Haemogamasus keegani* and *Hirstionyssus utahensis* have previously been reported from *Sorex trowbridgii* (see Whitaker and Wilson, 1974), but we did not find these species. New parasite records for this species are *Haemogamasus reidi*, *H. ambulans*, *Androlaelaps fahrenholzi*, *A. casalis*, *Eulaelaps stabularis*, *Eubrachylaelaps debilis*, *Alphalaelaps aplodontiae*, *Laelaps alaskensis*, *Orycteroxenus soricis*, *Glycyphagus hypudaei*, *Eucheyletia bishoppi*, and *Pygmephorus designatus*. New host records for *Sorex vagrans* are *H. occidentalis*, *H. reidi*, *Eulaelaps stabularis*, *Hirstionyssus obsoletus* (var.), *Alphalaelaps aplodontiae*, *Laelaps alaskensis*, and *Amorphacarus hengererorum*.

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Vegetation and Fire History of a Ponderosa Pine-White Fir Forest in Crater Lake National Park

Abstract

This paper describes the structure and composition of the vegetation, and some of the environmental factors controlling it, on 7.5 km^2 of Crater Lake National Park, Oregon. It also gives the approximate dates and locations of most fires that burned in the area between 1750 and 1902. We sampled the vegetation in 64 plots. Wedges cut from 49 fire scars revealed the dates of fires at 24 locations.

Eight communities occur in the four recognized habitat types. Soil formed in alluvial parent material supports the relatively dry *Abies concolor/Symphoricarpos mollis* habitat type. Pumice parent material supports an *Abies concolor/Chimaphila umbellata* habitat type, an *Abies magnifica* var. *shastensis* habitat type, and most of a Mesic Species community. *Abies* saplings on alluvial soils have considerably greater plant moisture stress than those on pumice. The Mesic Species community occurs in areas with the water table near the surface in the spring, which provides enough moisture to stop some fires. Two communities of the *A. concolor/C. umbellata* habitat type occur above and below the Mesic Species community; differences between them are probably due to different frequencies of fire before 1902 as well as to the climatic changes with elevation. Fires occurred at sampling spots at intervals of three or less to more than fifty years, with the mean interval at a location ranging from nine to forty-two years. The mean interval between fires was generally longer at higher elevations. Areas on opposite sides of a canyon usually did not burn in the same year, and fire years do not correspond with drought years indicated by previous dendrochronological studies. The occurrence of a widespread fire appeared to reduce the intensity or size of fires occurring in the same area in the following ten years. Most trees now present on the study area started growing during the first forty years after the last fire in 1902; compositional change in overstory and understory, apparently due to fire exclusion, is obvious in several communities.

Introduction

Much recent literature has emphasized the importance of fire in many of the primeval coniferous forests in North America (Arno, 1976; Habeck and Mutch, 1973; Heinselman, 1973; Kilgore, 1973a; Martin *et al.*, 1976; Weaver, 1974; Wright and Heinselman, 1973). The absence of fire because of fire control has led to major changes in forest vegetation. Fire is being re-introduced in many ecosystems as a management technique; returning the vegetation in National Parks toward its primeval state is one of the recent uses of fire (Kilgore, 1973a). To use fire successfully in management, certain information is necessary about each individual area, since the effect of fire depends on such things as weather, topography, fuels, vegetation, soils, and the intensity and frequency of the fires. The purpose of this study was to determine the present vegetation structure and composition (with an estimate of that in the primeval forest) and the fire history for an *Abies concolor-Pinus ponderosa* forest in Crater Lake National Park. This background information was to be used in the introduction of prescribed burning. This in-

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formation can also be used to find some characteristics of naturally occurring fires, and thus can contribute to an understanding of fire as a component of ecosystems and as a factor in evolution. The relationships of vegetation to fire and soils in the study area are probably representative of those over a considerable area in south central Oregon.

The Study Area

The study area is about 7.5 km^2, located just inside the south boundary of Crater Lake National Park, Oregon, at the base of the east slope of the Cascade Mountains. Except for the 15 to 60 m deep, ravine-like canyon of Annie Creek (Fig. 1), it has a fairly even slope averaging 3.5 percent between 1340 m elevation at the southern end and 1550 m at the northwest edge.

Most of the area was covered by a glowing avalanche deposit of pumice from an eruption of Mt. Mazama about 7000 years ago (Olsson, 1970; Rubin and Alexander, 1960; Williams, 1942). This eruption resulted in deposits of sub-rounded pumice cobble and gravel in a sand matrix. The soils on the pumice resemble the Lapine (Dyrness and Youngberg, 1966) and the Steiger series (U.S. Bureau of Indian Affairs *et al.*, 1958).

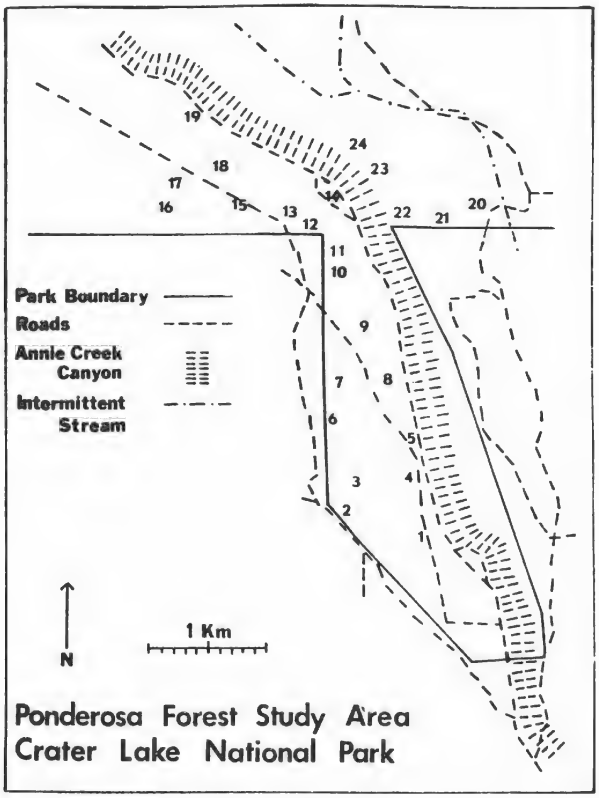

Figure 1. Spots where fire scars were sampled. The number refers to the data reported in Table 4. Two trees were sampled at each spot.

The pumice particles give the soil an unusually high porosity: it holds an unusually large amount of water at low tensions for a coarse-textured soil (Youngberg and Dyrness, 1964).

The area lies on the strong climatic gradient east of the Cascade Mountains (Franklin and Dyrness, 1973). The mean precipitation is probably between 65 and 85 cm yr^{-1} (U.S. Dep. Agr., 1964). About 70 percent falls from November to March and less than 10 percent falls from June to August (Sternes, 1963). It is probably safe to assume that the soil is at field capacity shortly after snowmelt, and that soil moisture declines through the summer.

Trappers first entered Klamath County about 1825, but there probably were no white settlements near the study area until about 1863, when a road was built through the area (Good, 1941). Crater Lake National Park was established in 1902, about the time the last fire burned in the area. The "panhandle," which includes much of the study area, was not added until 1932. Parts of this later addition had been logged between 1909 and 1927.

Methods

We sampled the vegetation in 64 plots, 50 of them randomly located along ten east-west transects, which had been selected in a stratified random manner. Fourteen plots were randomly located in vegetation units not adequately sampled on the transects. The data collected at each plot were similar to those of Daubenmire and Daubenmire (1968). All trees over 20 cm tall were tallied by diameter at breast height (dbh) class. Coverage of shrubs and herbs was recorded for each species in fifty 20 x 50 cm microplots. Classification was done in a manner similar to that described by Franklin, Dyrness, and Moir (1970). Nomenclature follows Hitchcock *et al.* (1955, 1959, 1961, 1964, 1969) and Peck (1961) for the few species not in Hitchcock *et al.*

The vegetation can be divided into habitat types based on what the climax dominants of each area appear to be (Daubenmire and Daubenmire, 1968). In the absence of climax forest, our best evidence of what the climax tree dominants probably would be is the density of small tress of the various species, their shade tolerance, and their apparent health. We assessed the probable shrub and herb dominants by the composition of the understory beneath a nearly closed canopy of the apparent climax dominants, *Abies concolor* or *A. magnifica* var. *shastensis*. The habitat types were sub-divided into communities with relatively homogeneous present vegetation.

Moisture stress of 1-2 m *Abies concolor* saplings was measured at one location in each of five communities before dawn on 17 September 1974, as the pressure potential of the xylem sap, using a pressure chamber (Scholander *et al.*, 1965).

A ground fire may kill a section of cambium at the base of a tree. The thin bark growing over the wound and the pitch which exudes from its edge make this tissue especially susceptible to damage by later fires. These fire scars were used to reconstruct the fire history of individual *Pinus ponderosa* trees. "Scar" or "fire scar" means the whole wound caused by several fires, and "sear" means the wound caused by an individual fire. Scars with a large number of sears were selected at 24 widely dispersed spots (Fig. 1). None were available in the logged area. At each spot two trees, usually within 100 m of each other, were sampled to insure that few fires would be missed, since not all fires sear all scarred trees (Arno, 1976). The fire history for each tree was found by

cutting a wedge from one side of the fire scar and counting the rings outside the individual sears. There were problems with narrow, missing or indistinct rings, insect holes, decay, and later fires destroying evidence of earlier sears. Even the most accurate dates could be off 2 percent of the difference between the date of the fire and 1974. There were sometimes inconclusive indications of a sear; we recorded these. Since fires often reduce growth rate drastically for a few years (Keen, 1937), we also recorded sudden decreases in ring width which occurred during an unusually long interval between sears. We cross-dated the fires to determine the probable dates for individual sears. This system probably gives accurate dates for large fires, but smaller fires are more likely to be dated inaccurately; small fires may be inappropriately grouped with other fires by this method.

Ages of trees of selected sizes along transects in three communities were determined at 20 cm from the ground with an increment borer. In order to estimate the relationship between age and population density, we assumed the distribution of ages within a size class in the vegetation data corresponds exactly to the distribution of ages in the age sample for that size class. For instance, if the ages of four trees of a given species in a given size class were determined, a quarter of the trees in the size class were assumed to be the same age as each of the four trees. The number of age determinations for a given size class of one species ranged from ten for the more common size classes to one for the rare ones within each community.

Results and Discussion

Vegetation

Four habitat types, with eight communities, were recognized and mapped (Fig. 2, Tables 1 and 2). The communities can be separated along gradients of moisture, elevation, and succession, and by type of soil parent material (Table 3). These gradients are not completely independent. Logging and fire history, and relative abundance and sizes of *Pinus* and *Abies* were used to estimate the position of each community on the successional gradient (Table 3).

The *Abies concolor/Symphoricarpos mollis* habitat type appears to be the driest (Table 3). It is on soil formed from sandy alluvium deposited after the collapse of Mt. Mazama. The soil in much of the *Melica* community is similar to the soil in the pumice flow; however, non-pumice gravel is present, varying from almost none to almost all of the gravel. Much of the soil in the logged *Symphoricarpos* community has a darker, thicker A1 horizon with a generally lower proportion of pumice. It is questionable whether *A. concolor* would be the sole climax tree dominant in the logged *Symphoricarpos* community (Table 2). However, disturbance often favors plants from drier communities (Franklin and Dyrness, 1973), and the abundant *Carex pensylvanica* may slow tree establishment (USDA Forest Service, 1972).

The *Abies concolor/Chimaphila umbellata* habitat type occurs on soil derived from pumice flow deposits, and, as is the case with the other types on pumice, apparently experiences little moisture stress. This habitat type differs from the one on alluvium in that it has much more *Pinus contorta* and *Salix scouleriana*; several species, including *Symphoricarpos mollis*, *Senecio integerrimus*, *Melica aristata*, and *Hieracium* spp. are less common here (Tables 2 and 3). This habitat type is relatively large and occurs over

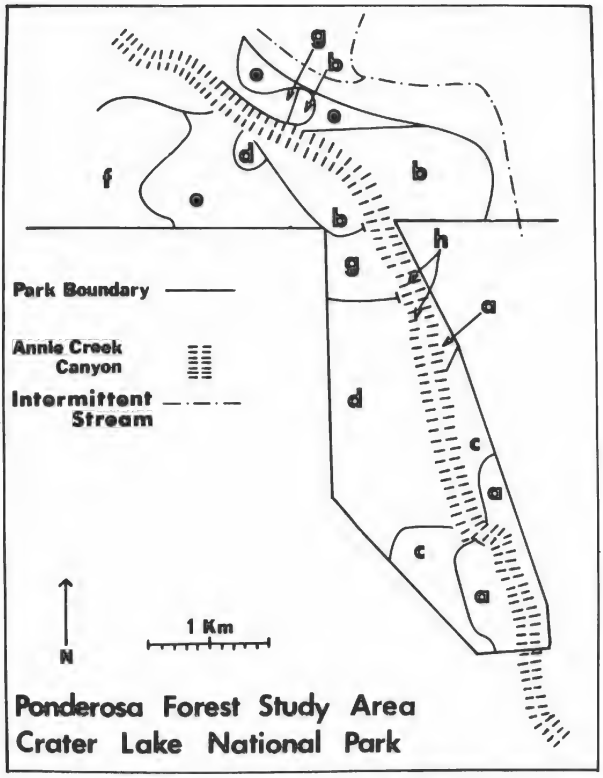

Figure 2. Location of plant communities and habitat types. *Abies concolor/Symphoricarpos mollis* habitat type: (a) Logged *Symphoricarpos mollis* community, (b) *Melica* community. *Abies concolor/Chimaphila umbellata* habitat type. (c) Logged *Chimaphila umbellata* community, (d) *Pinus lambertiana* community, (e) Closed *Abies concolor* community, (f) *Abies magnifica* var. *shastensis/Chimaphila umbellata* habitat type. *Abies concolor/* Mesic Species habitat type: (g) Mesic Species community, (h) *Castanopsis* community.

a greater range of elevation than the others. Differences in vegetation within it are probably caused by environmental differences as well as by differences in fire history. For example, *Arctostaphylos nevadensis* occurs only above *ca.* 1390 m, and *Apocynum androsaemifolium* rarely occurs above 1520 m. At lower elevations much of the *A. concolor* is in patchy, dense thickets of saplings, but at higher elevations it gradually becomes generally distributed. However, inferences about environmental causes are risky; elevation and disturbance are correlated, because the lowest elevations were logged, and the higher elevations were burned less frequently, giving it the aspect of a closed, relatively mature forest.

As one moves up in elevation within the *Abies concolor/Chimaphila umbellata* habitat types, the division between the *Pinus lambertiana* and the closed *Abies concolor* communities is approximately at the point at which understory dominants change from *Ceanothus velutinus* and *Arctostaphylos nevadensis* to mostly *Carex pensylvanica* and *Chimaphila umbellata* (Table 3). This division is also approximately where *Pyrola*

TABLE 1. Average density by species and community (trees/ha). Only trees taller than 20 cm are included.

Species	dbh class (cm)	Habitat Type: A. concolor/ Symphoricarpos		A. concolor/Chimaphila Community			Abies magnifica	A. concolor/ Mesic Species	
		Logged Symphoricarpos	Melica	Logged Chimaphila	Pinus lambertiana	Closed A. concolor	Abies magnifica	Mesic Species	Castanopsis
Populus	20-35	3							
tremuloides	10-20	63							
	0-10	872		129				128	
Calocedrus decurrens	0-10				16				
Pinus	95+				2				
lambertiana	55-75			4					
	20-35				2				
	10-20			4	9				7
	0-10			15	375				33
Pinus	35-55			11	4	16	18		
contorta	20-35			114	36	14	68	106	
	10-20			163	231	25	59	27	
	0-10			220	967	103	332		
Abies	95+						6		
magnifica	75-95						15		
var.	55-75						21		
shastensis	35-55					4	30		
	20-35					5	47		
	10-20				7	7	163		
	0-10		7		75	391	3970	10	
Pinus	20-35						3		
monticola	10-20					2	6		
	0-10					23	201	5	
Tsuga	10-20						3		
mertensiana	0-10				2	7	47		7
Pseudotsuga	95+								20
menziesii	75-95								26
	55-75								27
	35-55								14
	20-35								
	10-20					2			
	0-10				20				107
Pinus	95+		7		16	11	12	21	
ponderosa	75-95			4	11	14	9	10	

TARLE 1. (Continued)

Species	dbh class (cm)	Habitat Type: A. concolor/ Symphoricarpos		A. concolor/Chimaphila Community			Abies magnifica	A. concolor/ Mesic Species	
		Logged Symphoricarpos	Melica	Logged Chimaphila	Pinus lambertiana	Closed A. concolor	Abies magnifica	Mesic Species	Castanopsis
	55-75	27	7	19	7	2			7
	35-55	33		30	4			5	
	20-35	100		106	9				7
	10-20	170		99	4				7
	0-10	280		270	587	12			7
Abies	95+				2	2	3		7
concolor	75-95		7		2	5		3	27
	55-75	3	47			11	6	26	53
	35-55	27	87	15	7	68	16	70	7
	20-35	57	193	49	20	130	41	112	50
	10-20	213	247	137	209	338	98	373	86
	0-10	1282	2687	1003	2040	5118	3126	2592	1687

TABLE 2. Average percent cover and percent constancy of more important species. + = .05% or less. Only species occurring in more than two plots or with a mean cover of 0.1% are included. Data are presented as Cover/Constancy.

Species	Community: Logged Symphoricarpos	Melica	Logged Chimaphila	Pinus lambertiana	Closed A. concolor	Abies magnifica	Mesic Species	Castanopsis
Poa nervosa var. wheeleri	0.5/75							
Stipa occidentalis var. californica	0.1/50							
Senecio integerrimus	+ /50							
Lonicera conjugialis	0.5/63						0.1/40	
Lupinus albicaulis	0.6/75							+ /50
Melica aristata	0.6/50	0.3/50						0.1/50
Smilacina spp.	+ /38	+ /50					0.8/100	0.1/100
Ozmorhiza chilensis	+ /38	+ /25					0.5/80	0.1/75
Elymus glaucus	0.3/38	0.4/50		+ / 8			+ /40	+ /25
Phacelia heterophylla	0.1/63	+ /25	+ /14					+ /50

TABLE 2. (Continued)

Species	dbh class (cm)	Habitat Type: A. concolor/ Symphoricarpos		A. concolor/Chimaphila Community			Abies magnifica	A. concolor/ Mesic Species	
		Logged Symphoricarpos	Melica	Logged Chimaphila	Pinus lambertiana	Closed A. concolor	Abies magnifica	Mesic Species	Castanopsis
Stephanomeria lactucina	0.1/75	+ /25	0.2/43			+ /13			+ /25
Symphoricarpos mollis	3.0/88	1.4/100	+ /14			+ /20		2.1/100	6.0/100
Hieracium albiflorum + H. cynoglossoides	1.4/100	+ /73	+ /29					0.1/60	+ /100
Amelanchier alnifolia	2.8/38	0.1/25	+ /14					0.2/60	2.6/100
Bromus spp.	2.3/75		+ /29					1.3/100	0.5/75
Collomia tinctoria	0.1/38		+ /14						+ /25
Cynoglossum occidentale	+ /75		+ /29						+ /25
Purshia tridentata	0.6/75		+ /14						
Haplopappus bloomeri	1.9/100		0.3/43						
Ribes cereum	2.5/88		4.5/86						
Sitanion hystrix	2.9/88	+ /50	2.4/86						
Fragaria virginiana var. platypetala	1.2/100	0.3/100	1.4/100	+ /42		+ /47		0.2/80	+ /25
Kelloggia galioides	1.1/88	0.2/100	0.3/86	0.1/58		0.1/60		0.1/40	+ /50
Apocynum androsaemifolium	0.1/25	0.6/75	0.1/100	1.7/83		0.4/60		+ /40	0.1/25
Stipa occidentalis var. occidentalis	4.7/75	+ /50	4.9/100	0.6/75		+ /20	0.1/33		
Ceanothus velutinus	11.9/75	1.2/50	24.4/100	15.3/92		1.6/60	+ /11		+ /50
Arctostaphylos patula	+ /13		0.1/43	+ /33		+ / 7			+ /25
Epilobium angustifolium	0.1/50	0.1/75	0.9/100	0.6/67		+ /13	+ /22	+ /40	
Pyrola dentata	+ /13	+ /50	+ /57	0.1/75		0.1/80	+ /33	+ /20	
Salix scouleriana			4.2/71	2.1/92		0.5/47	+ /11	+ /60	
Polystrichum juniperinum		+ /25	0.4/57	+ /25		0.1/67	0.1/67		
Arctostaphylos nevadensis		0.5/25		8.6/83		3.3/73	5.7/89		
Pyrola secunda		+ /50	+ /43			0.5/100	0.1/56	0.5/100	0.1/50
Goodyera oblongifolia						+ /53	+ /22	0.1/80	
Castanopsis sempervirens	+ /13			0.7/33		+ / 7	+ /11	+ /20	6.3/100
Adenocaulon bicolor		+ /50						0.3/100	+ /100
Galium triflorum		+ /25						0.8/80	0.1/75

TABLE 2. (Continued)

Species	dbh class (cm)	Habitat Type: A. concolor/ Symphoricarpos		Habitat Type: A. concolor/Chimaphila Community			Habitat Type: Abies magnifica	Habitat Type: A. concolor/ Mesic Species	
		Logged Symphoricarpos	Melica	Logged Chimaphila	Pinus lambertiana	Closed A. concolor	Abies magnifica	Mesic Species	Castanopsis
Ribes viscosissimum			+ /50		+ / 8			0.9/60	0.2/75
Clintonia uniflora								0.6/60	0.1/50
Ribes lacustre								0.1/60	+ /75
Rubus parviflorus								+ /40	0.8/100
Rosa gymnocarpa	+ /13							+ /40	1.1/100
Pteridium aquilinum	+ /13								2.7/75
Carex pensylvanica + C. brainerdii	39.8/100	27.2/100	16.5/100	6.3/58		7.1/100	5.0/89	0.4/60	0.8/50
Chimaphila umbellata	+ /13	0.4/75	0.3/100	1.0/100		5.4/100	4.9/89	3.9/100	2.1/100
Chimaphila menziesii	+ /50	0.2/100	+ /57	+ /58		0.2/87	+ /89	0.1/100	0.2/100
Pyrola picta	+ /38	+ /25	+ /43	+ /42		+ /33	+ /22	+ /60	0.1/100
Brachythecium leibergii + Pohlia nutans	+ /13	0.2/50	+ /71	0.1/67		0.4/80	0.2/100	0.2/80	0.6/100
Pterospora andromedea	+ /38	+ /50	+ /71	+ /25		+ /40	+ /44	+ /40	
Antennaria rosea	0.2/38								
Gayophytum nuttallii	0.8/13		+ /43						
Corallorrhiza spp.						+ /40	+ /11		
Listera caurina		+ /25				+ / 7	+ /11	+ /40	
Anaphalis margaritacea								+ /40	+ /25
Eriogonum umbellatum	+ /38								
Melica subulata	+ /13	0.1/50							
Ruellia ruellii		+ /25				+ /13	+ /11		+ /25
Number of Plots	8	4	7	12		15	9	5	4

TABLE 3. Position of communities on gradients of soil, moisture, elevation, and succession. ND means not determined.

Community	Soil parent material	Predawn moisture stress (bars)	Elevation (m)	Relative successional stage
Logged Symphoricarpos mollis	Alluvial	-19	1340-1430	Early
Melica	Alluvial	-17	1430-1520	Late
Logged Chimaphila umbellata	Pumice	-7	1340-1410	Early
Pinus lambertiana	Pumice	ND	1370-1520	Middle
Closed Abies concolor	Pumice	-7	1480-1550+	Late
Abies magnifica	Pumice	-6	1510-1550+	Middle
Mesic species	Alluvial and Pumice	ND	1450-1550+	Late
Castanopsis	Alluvial	ND	1340-1450	Middle

secunda and *Goodyera oblongifolia* begin to occur, where *A. concolor* greater than 35 cm dbh become more important, and where small *Pinus ponderosa* almost disappear (Tables 2 and 3). Several understory plants, such as *Epilobium angustifolium* and *Salix scouleriana*, are less important at higher elevation. These changes are not sudden, and there are exceptions to the generalizations.

At higher elevations *Abies magnifica* var. *shastensis* becomes progressively more important. Where the *A. magnifica* var. *shastensis* less than 10 cm dbh outnumber *Abies concolor* of the same size, we recognize the *A. magnifica* var. *shastensis/Chimaphila umbellata* habitat type. Uncertainty about successional relationships of the two *Abies* necessitates the use of such an arbitrary distinction. Generally the understory is similar to the upper parts of the *A. concolor/Chimaphila* habitat type, with the sparse cover contributed by only a few species, except in some patches in which large *Pinus ponderosa* are located and *Arctostaphylos nevadensis* and *Carex pensylvanica* are fairly abundant (Table 3).

The *Abies concolor*/Mesic Species habitat type occurs in an area with the water table near the surface during the spring and in Annie Creek canyon. It contains several species that indicate moist conditions, such as *Smilacina* spp., *Adenocaulon bicolor*, *Galium triflorum*, and *Clintonia uniflora* (Table 3). The Mesic Species community separates the *Pinus lambertiana* and closed *Abies concolor* communities (Fig. 2). *Abies concolor* is the most important tree, but small areas have important components of *Pinus contorta* or *Picea engelmanni*, and there is a small meadow-like area. The *Castanopsis* community lies in Annie Creek canyon. *Pseudotsuga menziesii* is more important here than elsewhere. The top of the canyon often resembles the *Abies concolor/Symphoricarpos mollis* habitat type, and the vegetation becomes more mesic down into the canyon.

The vegetation is described in more detail by McNeil (1975); some communities recognized here result from combinations of the smaller ones he described.

Fire History

Fires rarely burned both east and west of Annie Creek during the same year (compare spots 20-24 with others in Table 4). The Mesic Species community stopped some fires from moving farther north (e.g., 1892, 1841, 1812), but did not stop others (e.g., 1902, 1879, 1846, 1818). So the area can be divided into three parts with different fire his-

TABLE 4. Fire incidence at different spots, 1748-1902. For spot locations, see Fig. 1. A. Each spot includes sears on two trees, usually within 100 m of each other. x = sear formed; (x) = possible sear formed—usually a growth rate decrease and some hint of sear present; map = sears at nearby spots indicate a fire may have burned this one also; interval = usually long interval without a fire; GR = decrease in growth rate that coincided with a fire year; . = date before the first sear on one tree at the spot; | = date before the first sear on both trees at the spot. B. Mean interval between fires, using (1) only definite sears, and (2) all indicators of fire occurrence.

A.	Panhandle										Northwest part									Northeast part			
Spot:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1902		x	x			map	x	x	x	x	x	x	x		x									.
1897								x						x										.
1892	x	map	x	x	x	x	x	x	x															.
1889																				x	x	x	map	x
1883	x	x	x								x													x
1879				x	x	x	x	x	x	x		x	x						x					.
1877																				x	x	x	x	x
1870	x		x						x												.			.
1864	x	x	x	map	x	x	x	x	x	x	x	x	x	x	x			map	x		.			.
1859																				x	GR		x	x
1855									x												.	interval		.
1849		x																			.			x
1846	x			x	GR	GR	x	(x)	x	map	x	x	x	x	x	x	x	x	x		.			.
1841	x	x	x	x	x	x	x	x	x		.			x	.					interval	.			.
1831											.				.						x	x	x	x
1829	x										.				.						.			.
1826					GR	GR		x	x		.	x			.		x				.			.
1818	x	map	x	map	x	map	x	map	x	x	x	x	x	x	x	x	x	x	x		.			.
1815											|				.	.					x			(x)
1812	x	x	x	x	x	x	x	x	x		|				.	.					.	x		.
1804	(x)										|	x	x		.	.		x			.			(x)
1800	x								interval		|				.	.		.	x		.			.
1798											|				.	.		.		x	x	x	x	.
1797	x	x	map	x	x	x	x				|				.	.		.			.	.		.
1791							x	x			|	x	x	x	x	.		.	x			.			.
1788											|		.	x	.	.		.			x	map	x	x
1786											|		.		.	.		(x)				.		|
1782-84	x		x		x	x	x		x	x	|	x	x		x	x	x	.			x	.		|
1779				interval	.					.	|		.	x	.	|		.				.	.		|
1776	GR	x			x			x		.	|		.		.			.				.	.		|
1775					.					.	|		.	x	.			.	x	(x)	x	.		|
1773					.			x		.	|		.		.			.	.		.	.		|
1771					.					.	|		.		.			.	.		x	.		|
1770					.					.	|	x	x		.		x	.	.		.	.		|

TABLE 4. Fire incidence at different spots, 1748-1902. For spot locations, see Fig. 1. A. Each spot includes sears on two trees, usually within 100 m of each other. x = sear formed; (x) = possible sear formed—usually a growth rate decrease and some hint of sear present; map = sears at nearby spots indicate a fire may have burned this one also; interval = usually long interval without a fire; GR = decrease in growth rate that coincided with a fire year; . = date before the first sear on one tree at the spot; | = date before the first sear on both trees at the spot. B. Mean interval between fires, using (1) only definite sears, and (2) all indicators of fire occurrence.

A.	Panhandle										Northwest part									Northeast part			
1769	x	x	x	x	x	x			GR	.			.		.				.	.		.	.		
1762			.		.					.			.		(x)				.	.		.	.		
1759	x		x		x	map	x	x	x	.		x	x	x			x		.	.	x	x	x	x	
1755	x		.	x	|					.		.	.					.	.	.		.	.		
1751			.		|					.		.	.					.	.	.	x	x	x	x	
1748			.		|	x	x	x	x	x		x	.					x	x	x		.	.	.	|
B. Mean interval between fires.																									
(1) Sears only	9	14	15	15	15	18	12	14	13	30	19	14	18	15	28	42	22	33	18	22	—	23	22	—	
(2) All indicators	9	12	13	12	12	12	11	12	12	24	19	14	18	15	28	42	22	24	18	19	—	18	20	—	

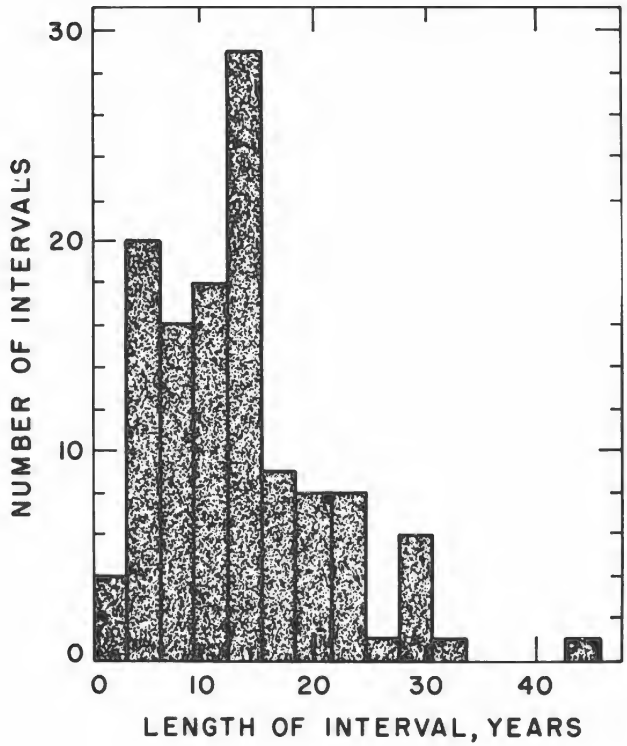

Figure 3. Frequency distribution of intervals between sears on fire scars in the panhandle area.

tories: 1) the panhandle; 2) the northwest part; and 3) the northeast part. The difference between the "long" and "short" estimates for the mean interval between fires at a spot (Table 4) is small when compared with the variance of intervals between fires (Fig. 3). These means are comparable to those found in other parts of Central Oregon (Keen, 1937; Sherman, 1969; Soeriaatmadja, 1965) and somewhat longer than in the mixed conifer forest for the Sierra Nevada (Wagener, 1961; Kilgore, 1973a). In order to maintain a "natural" mosaic of communities with prescribed fire, it may be necessary to imitate the frequency distribution rather than just the mean interval. For instance, intervals of 15 years or more without fire were not uncommon (Fig. 3). These spots may have provided refuge for species poorly adapted to fire—for example, those which require that long to reproduce.

Fire frequency and vegetation are correlated to some extent. Fire incidence decreases with increased elevation toward the northwestern part of the study area (Table 4, Fig. 1). It is somewhat lower in the Mesic Species community than immediately above or below. *Ceanothus velutinus* is dominant only where the mean interval between fires was 15 years or less, and it is almost absent where the interval was greater than 20 years. Others have noted that fire history can cause important differences in vegetation in this region (Dyrness and Youngberg, 1966; West, 1969).

Comparison of the dates of the fires with Keen's (1937) dendrochronological record for south central Oregon indicates that there is little relation between the years that fires occurred and those in which *Pinus ponderosa* growth was less than average, which Keen concludes are the drier years. Of forty fire years, sixteen had growth less than average; eighteen had better than average growth; the other six were very close to average. Of seventeen years with extensive fires (those which left sears at more than half the spots in one of the three parts of the study area), seven had greater than average growth. The inference that fires are not limited to the driest years is supported by the occurrence of fires in different years on the two sides of Annie Creek (Table 4). Years dry enough to allow extensive fire appear to have been fairly common.

One factor controlling the intensity and size of a fire is the fuel accumulation since the last fire. Evidence for its effectiveness occurred in our data. The upper limit to the percentage of trees seared by a major fire increases with time since the last large fire (Fig. 4). This effect can be seen by comparing the panhandle and the northwest part for the 1846 and 1818 fires (Table 4): these fires were apparently less intense, scarring fewer trees, in the panhandle where a large fire had recently burned.

Parts of the closed *Abies concolor* community have not burned since 1846, probably

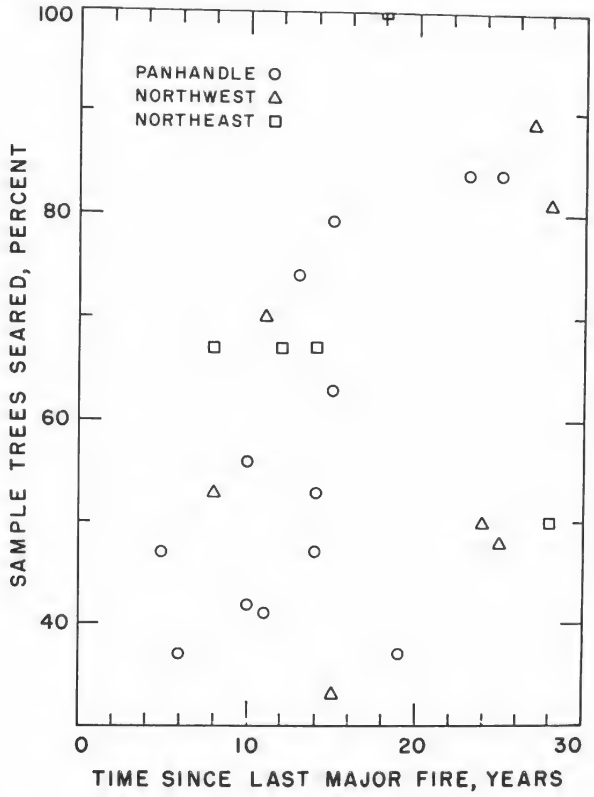

Figure 4. Relationship between years since last major fire and the proportion of sampled trees that were scarred, for all major fires between 1748 and 1902.

accounting for its high density of *Abies* and its sparse understory. The fact that fire did not occur here from 1846 to 1902 and that there are few 10-55 cm dbh *Pinus ponderosa* may indicate that this area would become dominated by *A. concolor* even without fire control.

Because of the small size and irregular shape of the study area, little can be said about the size of the fires. The large fires burned outside the study area, so their area is more than the 400 ha west of Annie Creek. Many of the small fires may also have burned outside the study area. From 1800 to 1902 there were about 15 fires that seared three or more adjacent spots; however, 12 to 16 or more fires seared only one or two spots that were well separated from any other spots seared the same year. This large number of small fires is somewhat surprising, because between 1930 and 1974 only two lightning fires were recorded in the study area (Fire Atlas, Crater Lake National Park). However, in each of the two years of this study we observed one large *Pinus ponderosa* killed by lightning, so lightning strikes probably are fairly common.

Effects of Fire Exclusion

Figure 5 shows the tree age-density relationships for one community. These and sim-

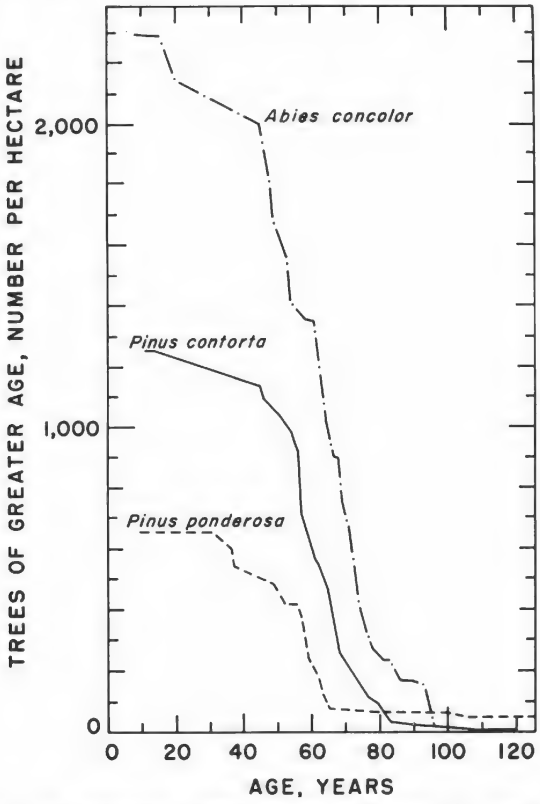

Figure 5. Estimate of the relationship between tree age and density for major trees in the *Pinus lambertiana* community. The position of the line for a given year represents the density of all trees that age and older.

ilar data from other communities indicate that most of the trees over 20 cm tall germinated within 30 or 40 years after the last fire; since then establishment of trees has decreased. It appears that *Abies concolor* may have become established more rapidly after the last fires than *Pinus ponderosa* or *Pinus contorta*, but this finding may be an artifact resulting from difficulty of counting rings in these severely suppressed *Pinus*. Repeated fire would have favored *Pinus* (Kilgore, 1973b; Lunan and Habeck, 1973), probably because of the thick bark of some species (Franklin and Dyrness, 1973) and their low shade tolerance (Atzet and Waring, 1970). Other changes are taking place in the understory due to increased shade or litter accumulation; for example, dead shrubs of *Ceanothus* and *Arctostaphylos* are common in areas where a closed *Abies* canopy has recently been established.

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A Listing of Reports on Black-Footed Ferrets in Wyoming (1851-1977)

Abstract

One hundred and forty-eight black-footed ferret (*Mustela nigripes*) reports from Wyoming (1851-1977) are recorded, complete with an evaluation of each.

Black-footed ferrets (*Mustela nigripes*) are one of North America's rarest mammals (Cahalane, 1954; Linder and Hillman, 1973; Clark, 1976). In states which are undergoing rapid change through energy and mineral development and mushrooming human population, information is imperative on rare, threatened, and endangered species for distribution to the largest possible audience. From knowledge of the distribution and precarious situation of this species, plans can be made to minimize human impacts on them. Comprehensive ferret listings for several states have been published, but none currently exists for Wyoming. The first listing of eight Wyoming ferret reports was by Long (1965). Hershkovitz (1966) reported seeing a ferret in central Wyoming. Clark (1973) gave 18 additional reports. The first major effort to collect and evaluate ferret reports in Wyoming was initiated in 1973 (Clark, 1978). The increased number of reports in recent years does not reflect an increase in ferrets, but instead a growing concern for the animal's decreasing numbers. The following list of 148 reports gives ferret information from 1851-1977.

The following table gives all those ferret reports which appeared to be positive or probably so. Each report was classified as: 1) *Positive*—if the observer showed physical evidence (*e.g.*, skin, photograph or ferret trenches); or if he was a biologist or professional field-oriented worker (*e.g.*, geologist, range manager), if the region had a documented history of ferret sightings, and if the habitat was characterized by abundant ground-dwelling sciurids (especially prairie dogs). If the sighting was in white-tailed prairie dog habitat, presence of suitable alternate prey during winter was required. 2) *Probable*—if the observer gave an accurate description, identified a ferret from a series of mustelid pictures, and characterized the animal's behavior in detail. The report had to be supported by other independent sightings, or other evidence of ferrets in the immediate area.

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TABLE 1. A Listing of Black-Footed Ferret (*Mustela nigripes*) Reports in Wyoming 1851-1977.

No.	Date	Location	Animal(s)	Source	Comments
1.	1851	Ft. Laramie, Goshen Co.	1 ad	Audubon and Bachman	Type Specimen, Skin in USNM; Positive
2.	1877	Cheyenne Depot, Laramie Co.	1 ad?	Capt. Gilliss	Record by Coves in a book on "Fur Bearing Animals"; Positive
3.	1880s or earlier	N. Wyo. or S. Mont. in range of Crow Indians	8 ad?	Tim Clark	4 in Plains Indian Mus., Pryor, Mont. Mus., Cody, Wyo; 4 in Chief Plenty Coups Positive
4.	1883 1 Dec	Duck Creek, 12 mi from Cheyenne, Laramie Co.	1 ad?	John Mason and Charles Ruby	Skin (#13996) and skull (#21066) in USNM, Positive
5.	1895 1 May	New Castle Weston Co.	1 ad female	Frank Bond	Skin (#71750) in USNM; Positive
6.	1902	Shirley Mts. Carbon Co.	1 ad?	R. J. Lentz	Positive
7.	1910	New Castle, Weston Co.	1 ad?	S. E. Piper	Skull in USNM; Positive
8.	1911 spring	Redwater Creek near Beulah, Crook Co.	1 ad male	M. Cary (#247)	Skin and skeleton in USNM (#180719); Positive
9.	1911 Oct.-Nov.	Clear Creek above Big Red, Co.?	1 ad?	M. Cary	Skin in USNM (#180718), killed by C. Lawrence; Positive
10.	1916 14 April	Manville, Niobrara Co.	1 ad male	R. T. Jackson (#14055)	Skin and skull in USNM (#211513), Positive
11.	1917 9 Sept.	Douglas, Converse Co.	1 ad male	E. Freeman (#19699)	Skin and skull in USNM (#227703), Positive
12.	1920s	10 mi S Tensleep, Washakie Co.	2 ad?	G. Taylor	Probable
13.	1920	Near Ft. Bridger, Uinta Co.	1 ad?	W. Casto	Probable
14.	1920 spring	1 mi SW Lander, Fremont Co.	1 ad?	H. J. States	Caught in coyote trap, Positive
15.	1923 summer	35 mi S and 10 mi W Gillette (T42N-R74WS27), Campbell Co.	1 ad?	U. S. Archibald	Positive
16.	1923 winter	11 mi NW Laramie, Albany Co.	1 ad	V. A. Collins	Caught in coyote trap, Positive
17.	1924 20 Oct.	5 mi W Laramie, Albany Co.	1 ad male	A. M. Day (#23810)	Skin and skull in USNM (#245641), Positive
18.	1925 summer	35 mi S and 10 mi W Gillette (T42N-R74WS27), Campbell Co.	1 ad	U. S. Archibald	Positive
19.	1930	Four Horse Creek, S Morecroft, Crook Co.	1 ad	B. Barker	Positive
20.	1930	Niobrara Co.	1 ad?	R. Freeman	Positive
21.	1930	5 mi E Farson and 2 mi S (T25NR106W-S12), Sweetwater Co.	1 ad	F. Meyer	Caught in badger trap, Positive
22.	1930s	Cottonwood Creek, Hot Springs Co.	several	D. Ramul	Trapped several, Probable

TABLE 1. (Continued)

23.	1930 ca	12 mi SE Casper, Natrona Co .	1 ad	H. Lamb	Caught in badger trap, Positive
24.	1930 ca	18 mi SW Upton on Deep Water Creek, Weston Co.	1 ad?	W. Butolph	Positive
25.	1930 ca	"Park Co.?"	2 ad	B. Edgar	In collection at Old Trail Town, Cody, Positive
26.	1932-1936	Converse Co.	7 or 8	D. Fortenbery	Caught in coyote traps by L. Hutchinson, Positive
27.	1933	Wheatland, Platte Co.	1 ad?	R. Hubbard	Observed catching millers under street light at town's edge, Positive
28	1933	N Cheyenne, Laramie Co.	1 ad?	A. Hume	Captured one, Positive
29.	1933-1935	12 mi NW Laramie, Albany Co.	several	F. Carroll	Positive
30.	1934	E Medicine Bow, Carbon Co.	1 ad?	P. Muchmore	Captured one, Positive
31.	1935	14 mi N Lister Sheridan Co.	1 ad male	J. V. Fillmore	Skin preserved, captured in coyote trap by Govt. trapper, Positive
32.	1939 Nov.	Foot Eagle Peak W of Laramie Peak, Albany Co.	1 ad	D. Prager	Skin preserved, Positive
33.	1940	5 mi NW Lander, Fremont Co.	1 ad?	T. Bell	Positive
34.	1942 summer	35 mi S and 10 mi W Gillette (T41N-R74WS7), Campbell Co.	1 ad	U. S. Archibald	Positive
35.	1942	N Garett, Albany Co.	1 ad?	D. Prager	Positive
36.	1947 August	15 mi S LaBarge, Lincoln Co.	1 ad?	L. Leisinger	Probable
37.	1948	Niobrara Co.	1 ad?	C. R. Mueller	Reported by Cahalane (1954), Positive
38.	1948	Near Shawnee, Platte Co.	1 ad?	C. R. Mueller	Reported by Cahalane (1954), Positive
39.	1948 July	ca 3 mi SW of Woodrow Peterson Ranch, Crook Co.	1 ad?	G. Prazma	Positive
40.	1949 summer	7 mi W Laramie, Albany Co.	1 ad?	A. M. Day	Positive
41.	1949 summer	Cottonwood Creek, Teton Co.	1 ad?	J. and F. Craighead	Positive
42.	1950s	Oregon Butte, Sweetwater Co.	4 as singles	D. Henderson	Positive
43.	1950	1.5 mi W Laramie, Albany Co.	1 ad	R. W. Fautin	Road killed, Positive
44.	1950 summer	N Devil's Tower, Crook Co.	1 ad?	C. Dickinson	Positive
45.	1950 summer	N Campbell Co.	1-2 ad?	C. Dickinson	Positive
46.	1952 summer	20 mi SW Thermophilus, Hot Springs Co.	1 ad?	B. Milek	Positive

TABLE 1. (Continued)

47.	1955 summer	7.5 mi S Jeffery City, T28NR90WS20, Fremont Co.	1 ad?	W. A. Street	Positive
48.	1955 summer	23 mi S Tensleep, Washakie Co.	1 ad?	P. Mortensen	Positive
49.	1955 Sept.	17 mi NE Saratoga, T19NR83WS15, Carbon Co.	1 ad?	A. Welton	Probable
50.	1955	Hot Creek Basin to Lusk vicinity, Niobrara Co.	1 ad?	J. Clark from E. Bakko	Positive
51.	1955 ca	In basement in house, Laramie, Albany Co.	1 ad?	R. W. Fautin	Shot by Fautin, skin at Univ. Wyoming, Positive
52.	1956	W Saratoga, Carbon Co.	1 ad?	J. States	Positive
53.	1956 June	3 mi SW Encampment, T15NR84WS15, Carbon Co.	1 ad?	D. Cruse	Positive
54.	1957 summer	5 mi SE Lander, T32NR93WS11, Fremont Co.	1 ad?	J. States	Positive
55.	1957 or 1958 Sept.-Oct.	SW Farson, Sweetwater Co.	3 young	F. Christensen	Playing alongside road in a 6″ culvert, Positive
56.	1959	8 mi SE Riverside, Carbon Co.	1 ad?	C. Heinrich	Probable
57.	1960	T15NR76WS?, Albany Co.	1 ad?	O. Schmidt to E. Bakko	Positive
58.	1961	12 mi SW Laramie, Albany Co.	1 ad and 2 young	"Rancher" to R. Fautin	Positive
59.	1963	10 mi S Wamsutter, Sweetwater Co.	1 ad?	R. J. Murphy	Positive
60.	1963	40 mi N Laramie, Albany Co.	1 ad?	R. J. Murphy	Positive
61.	1963 Sept.	Just W Chugwater, Platte Co.	1 ad?	R. J. Lentz	Positive
62.	1964 Sept.	T14NR75WS21, Albany Co.	1 ad?	H. Banzhaf to E. Bakko	Positive
63.	1964 May	T15NR76WS36, Albany Co.	1 ad?	L. Atkinson to E. Bakko	Positive
64.	1964 June	T14NR77WS7 Albany Co.	1 ad?	D. Turner to E. Bakko	Positive
65.	1964 July	T14NR78WS11, Albany Co.	1 ad?	K. Langford to E. Bakko	Positive
66.	1964 summer	Foot Eagle Peak, W of Laramie Peak, Albany Co.	1 ad?	D. Prager	Positive
67.	1964 Aug.	T19NR74WS11, Albany Co.	1 ad?	J. Wallis to E. Bakko	Positive
68.	1964 22 Aug.	10 mi S Medicine Bow, Carbon Co.	1 ad?	R. Gerhardt to E. Bakko	Positive
69.	1964 Nov.	10 mi W Chugwater, Platte Co.	1 ad?	J. Hitt to E. Bakko	Positive
70.	1965 29 June	6 mi E Casper, Natrona Co.	1 ad?	P. Hershkourtz	Positive
71.	1965	5.3 mi N Farson, Sweetwater Co.	1 ad?	F. Glover	Positive
72.	1965 summer	130-230 Hwy Junction 8 mi S Saratoga, Carbon Co.	1 ad?	F. J. Legoski	Positive

TABLE 1. (Continued)

73.	1966 summer	6 mi N Pine Bluffs, Laramie Co.	1 ad?	P. Mortensen	Probable
74.	1967	Happy Jack area, Laramie Mts, Albany Co.	1 ad?	G. Erickson	Probable
75.	1968 May	2 mi S Green River 2 mi off River, Sweetwater Co.	1 ad?	R. Larimore	Probable
76.	1968 Aug.	2.5 mi N Lander, T34NR99WS31, Fremont Co.	1 ad?	T. R. Bell	Positive
77.	1968 ca	18 mi W Thermophilus, Hot Springs Co.	1 ad?	L. Shumway	Probable
78.	1968	25 mi W Thermophilus, T8NR2ES34, Hot Springs Co.	1 ad?	P. Long	Probable
79.	1968	2-3 mi W Medicine Bow, Carbon Co.	2 ad?	P. Riddle	Positive
80.	1968 fall	W Side Sheep Mt. on Albany Co. Rd., Albany Co.	1 ad?	J. Coykendall	Probable
81.	1969	Crook Co.	1 ad?	G. Roby	Positive
82.	1969	T18NR93WS21, Sweetwater Co.	1 ad?	F. Belcher	Positive
83.	1969 Sept.	Near I80 & Herrick Lane underpass, Albany Co.	1 ad?	J. Coykendall	Probable
84.	1969 fall	Near Arlington, Carbon Co.	1 ad?	P. Holloway	Probable
85.	1969 winter	5 mi W Saratoga, Carbon Co.	1 ad?	L. Garetson	Probable
86.	1970 summer	25 mi W Thermophilus, Hot Springs Co.	1 ad?	H. B. Rathburn	Probable
87.	1971	Near Union Pacific RR tracks; ca 10 mi W Rawlins, Carbon Co.	1 ad?	R. Corsi	Positive
88.	1971	Middle-Osage Comm. Pasture, Crook Co.	1 ad?	G. Roby	Positive
89.	1971	2 mi E Rawlins, Carbon Co.	1 ad?	M. Sawyers	Probable
90.	1971	N Medicine Bow, Carbon Co.	1 ad?	L. Anderson	Positive
91.	1972	ca 5 mi S US 16 where it enters Wyo. from S.D., Weston Co.	1 ad?	C. Hillman	Positive
92.	1972 21 June	T21NR112WS29, on Hwy 30 near Opal, Lincoln Co.	1 ad?	M. Wilson	Positive
93.	1972 June	1.5 mi SE Lovell Lake, T56NR95WS32, Big Horn Co.	1 ad?	J. Brinderhoff	Positive
94.	1972 July	4 mi E Dubois, Fremont Co.	1 ad?	Audubon Sci. Camp personnel	Positive
95.	1972 July	Delanie Rim, SW Rawlins, Carbon Co.	2 young	M. May	Positive
96.	1972 July-	20 mi NE Lysite, Natrona Co.	1 ad	I. T. Metzler	Positive

TABLE 1. (Continued)

97.	1972 August	2 mi N Riverside on Hwy 230, T15N-R84WS36-31, Carbon Co.	1 ad?	W. J. Freshman	Positive
98.	1972 August	T14NR98WS36-35, Sweetwater Co.	1 ad?	B. McMahan	Probable
99.	1972 8 Aug.	T50NR88WS25, Near Hyattville, Big Horn Co.	1 ad?	R. W. S. Musgrave	Probable
100.	1972 20 Aug.	25 mi E Thermophilus, T14NR93WS10, Hot Springs Co.	1 ad?	B. Milek	Positive
101.	1972 August	T26NR83WS17, Carbon Co.	1 ad?	D. Wheeler	Dead in stock tank, Positive
102.	1972 summer	1.5 mi SE Lovell Lake, T56NR95WS32, Big Horn Co.	1 ad?	C. Kober	Positive
103.	1972 October	S John Hay Res., T25NR98WS26, Sweetwater Co.	1 ad?	D. Randall	Positive
104.	1972 winter	T41NR69WS21, Converse Co.	1 ad?	D. Irwin	Probable
105.	1973 May	3 mi E Riverside & 1.2 mi S, T14NR83W-S9, Carbon Co.	1 ad?	B. Gallup	Positive
106.	1973 June	7 mi S Lovell, Big Horn Co.	1 ad?	A. Rodrigues	Probable
107.	1973 12 June	7.5 mi S Jeffery city, T28N90WS20, Fremont Co.	1 ad?	W. A. Street	Positive
108.	1973 June	20 mi NE Lysite, T39NR88WS15, Natrona Co.	1 ad?	J. Sutton	Probable
109.	1973 5 July	6-8 mi N Farson, Sweetwater Co.	1 ad?	T. Costin	Positive
110.	1973 July-Sept.	20 mi NE Lysite, Natrona Co.	1 ad?	I. T. Metzler	Positive
111.	1973 August	20 mi W LaBarge, Lincoln Co.	1 ad?	A. Reynolds	Probable
112.	1973 August	4 mi E Dubois, Fremont Co.	1 ad?	6 people from Audubon Sci. Camp, R. Turner	Positive
113.	1973 22 Sept.	25 mi W Thermophilus, Hot Springs Co.	1 ad?	G. Gamble	Probable
114.	1973 29 Sept.	3 mi E Crook-Campbell Co. line and 8 mi N I90, Crook Co.	1 ad?	S. Dillinger	Probable
115.	1973 Sept.	8 mi SE Riverside, T14NR83WS?, Carbon Co.	1 ad?	C. J. Heinrich	Probable
116.	1973 Sept.	10 mi N LaBarge, Sublette Co.	1 ad?	W. Yose	Probable
117.	1973 12 Oct.	0.5 mi NE Albany Co., Water Treatment Plant (Hwy 230), Albany Co.	1 ad?	T. Cram	Positive
118.	1974 17 May	9 mi E on Wyo 351 from Route 189 (Big Piney Cutoff), Sublette Co.	1 ad?	K. McNinch	Probable

119.	1974 June	3-5 mi E Powder River, Johnson Co.	1 ad?	D. Jones	Positive
120.	1974 June	4 mi N Saratoga, Carbon Co.	1 ad?	J. Roth	Probable
121.	1974 July	ca 4 mi E Woods Landing, Albany Co.	1 ad?	L. Garetson	Probable
122.	1974 July	Lower Prairie Dog Rd on Mont-Wyo line, Sheridan Co.	1 ad?	C. Saddler	Probable
123.	1974 16 July	3 mi NE Encampment T15NR83WS1, Carbon Co.	1 ad?	J. Bellar	Positive
124.	1974 19 July	20 mi NW Laramie on I80, Albany Co.	1 ad?	M. Hornocker	Positive
125.	1974 28 July	20 mi E Worland, Washakie Co.	1 ad?	D. M. Fritz	Positive
126.	1974 29 July	10 mi W Reno Junct., T43NR73WS5, Campbell Co.	1 ad?	J. Heasley	Positive
127.	1974 July	5-10 mi E of Powder River, Natrona Co.	1 ad?	D. Jones	Positive
128.	1974 1 Aug.	20 mi S and 10 mi E Tensleep, Washakie Co.	1 ad?	L. Kapptie	Probable
129.	1974 15 Aug.	8 mi SE Saratoga at RR tracks near 230-130 Hwys, Carbon Co.	1 ad?	N. J. Miller	Probable
130.	1974 17 Aug.	1 mi W New Fork R. Bridge on Big Piney Cutoff Sublette Co.	1 ad?	L. E. TenEyck	Probable
131.	1974 21 Aug.	Midway between Big Piney and LaBarge, Sublette Co.	1 ad?	D. Roden	Probable
132.	1974 10 Sept.	5 mi S Bitter Cr., T18NR88WS30, Sweetwater Co.	1 ad?	A. Keeney	Probable
133.	1974 Sept.	2 mi E Centinnial, Albany Co.	1 ad?	M. Hagen	Probable
134.	1974	T20NR11WS30, NW¼, Sweetwater Co.	1 ad?	W. Hollingworth	Probable
135.	1975 April	T15NR83WS30, near Encampment, Carbon Co.	1 ad?	S. Knotwell	Probable
136.	1975 May	10 mi S Arvada on Powder River, Sheridan Co.	1 ad?	G. Sorenson	Positive
137.	1975 29 May	Between Hiland and Moneta on Lynn Ranch Matador Cattle Co., Natrona Co.	1 ad?	M. Sullivan	Probable
138.	1975 August	9 mi S Daniel on Cottonwood Creek, Sublette Co.	1 ad?	C. James	Probable
139.	1975 August	6 mi NE of Encampment, Carbon Co.	1 ad?	T. Demment	Positive
140.	1975 August	10 mi N Tensleep, Washakie Co.	1 ad?	G. Johnson	Positive
141.	1975 October	T21NR111WS1, Sweetwater Co.	1 ad?	D. Lockman	Positive
142.	1976?	T22NR110WS22, Sweetwater Co.	1 ad?	J. June	Positive

143.	1976 15 May	T43NR70WS30, Campbell Co.	1 ad?	J. Tate	Positive
144.	1976 summer	Between Pt. of Rocks and Hallville (near Black Butte), Sweetwater Co.	1 ad?	M. Long	Probable
145.	1976 August	ca 25 mi NNW of Casper, Natrona Co.	1 ad?	G. Johnson	Probable
146.	1976 October	15 mi N Midwest, Johnson Co.	1 ad?	I. Samson	Positive
147.	1977 June	ca 5 mi S Rawlins, T21NR89WS35, NE¼, Carbon Co.	1 ad?	J. Weaver	Positive
148.	1977 July	T31NR109WS33, Sublette Co.	1 ad?	F. Owner	Probable

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A Partial Bibliography of Wyoming Mammals

Abstract

Recent literature recognizes 106 native mammal species in Wyoming. There is a growing need for resource managers and others to have a good overview and ready access to the mammal literature in states which are undergoing massive environmental changes, as is the case with Wyoming. This bibliography lists 316 papers on these species, excluding man, up to 1976. Six journals (Journal of Mammalogy, Journal of Wildlife Management, Southwestern Naturalist, Northwest Science, American Midland Naturalist, and Ecology) and other sources (monographs, theses from area universities, and state and federal agencies) were searched.

Introduction

Recent literature recognizes 106 native mammal species in Wyoming. As recently noted by Casey and Clark (1978),[1] there is a growing need for resource managers and others to have a good overview and ready access to the mammal literature in states which are undergoing massive environmental changes. This bibliography lists 316 papers on these species, excluding man, up to 1976, in the state of Wyoming. Six journals (J. Mammalogy, J. Wildlife Management, Southwestern Naturalist, Northwest Science, American Midland Naturalist, and Ecology) and other sources (monographs, theses from area universities, and state and federal agencies) were searched. Although our list is not complete, it does represent the bulk of the references on Wyoming's mammals.

Our bibliography is organized into three parts. Part one gives a numbered taxonomic listing of species, excluding *Homo sapiens*, grouped by order and family. Part two is a numbered listing of taxa larger than species (e.g., Mustelidae) and general subjects (e.g., carnivores). Part three is the numbered bibliography proper and is cross-referenced to the species and general subject lists. Taxonomy follows Long (1965).[2]

[1]Casey, D. E., and T. W. Clark. 1978. An analysis of the journal literature on Wyoming mammals. Northw. Sci. 52(3): 272-275.

[2]Long, C. A. 1965. The mammals of Wyoming. U. Kans. Mus. Nat. Hist. Publ. 41:493-758.

O. Marsupialia—Marsupials
F. Didelphidae—Opossum
1. *Didelphis marsupialis*—opossum (39)
O. Insectivora
F. Soricidae—Shrews
2. *Sorex cinereus*—masked shrew
3. *Sorex vagrans*—vagrant shrew (123)
4. *Microsorex hoyi*—pygmy shrew (41, 196, 198)
5. *Sorex nanus*—dwarf shrew (217)
6. *Sorex palustris*—water shrew (48, 49, 84, 185)
7. *Sorex merriami*—Merriam shrew (35, 216)
F. Talpidae—Moles
8. *Scalopus aquaticus*—eastern mole
O. Chiroptera—Bats
F. Vespertilionidae
9. *Myotis lucifugus*—little brown myotis
10. *Myotis subulatus*—small-footed myotis (259)
11. *Myotis volans*—long-legged myotis (259)
12. *Myotis evotis*—long-eared myotis
13. *Myotis keenii*—Keen myotis
14. *Lasionycteris noctivagans*—silver haired bat
15. *Lasiurus borealis*—red bat
16. *Lasiurus cinereus*—hoary bat
17. *Plecotus towsendi*—Towsend bat
18. *Euderma maculatum*—spotted bat (218)
19. *Eptesicus muscus*—Big brown bat (121, 194)
O. Lagomorpha—Pikas, Rabbits & Hares
F. Ochotonidae—Pikas
20. *Ochotona princeps*—pika (220, 271)
F. Leporidae—Rabbits & Hares
21. *Sylvilagus floridanus*—eastern cottontail
22. *Sylvilagus nuttalli*—mountain cottontail (151)
23. *Sylvilagus audubonii*—desert cottontail (177)
24. *Lepus americanus*—snowshoe hare (28, 181)
25. *Lepus townsendi*—white-tailed jackrabbit (273)
26. *Lepus californicus*—black-tailed jackrabbit
O. Rodentia—Rodents
F. Scuiridae—Squirrels
27. *Eutamias minimus*—least chipmunk (277, 279)
28. *Eutamias amoenus*—yellow-pine chipmunk
29. *Eutamias dorsalis*—cliff chipmunk
30. *Eutamias umbrinus*—Uinta chipmunk (310)
31. *Marmota flaviventris*—yellow-bellied marmot (21, 22, 24, 131, 250, 297)
32. *Spermophilus richardsoni*—Richardson ground squirrel (54, 56, 57, 59, 111, 112, 113, 114, 246, 247)
33. *Spermophilus armatus*—Uinta ground squirrel (85, 187, 246, 247, 304)
34. *Spermophilus spilosoma*—spotted ground squirrel (246, 247)
35. *Spermophilus tridecemlineatus*—thirteen-lined ground squirrel (55, 60, 246, 247)
36. *Spermophilus lateralis*—golden-mantled ground squirrel (246, 247, 278)
37. *Cynomys ludovicianus*—black-tailed prairie dog (65, 66, 69, 71, 172, 266, 303)
38. *Cynomys leucurus*—white-tailed prairie dog (29, 30, 58, 65, 66, 69, 71, 168, 172, 266, 286, 287, 303)
39. *Tamiasciurus hudsonicus*—red squirrel
40. *Sciurus niger*—fox squirrel
41. *Sciurus aberti*—tassel-eared squirrel (Abert's) (37)
42. *Glaucomys sabrinus*—northern flying squirrel (175)
F. Geomyidae—Pocket Gophers
43. *Thomomys talpoides*—northern pocket gopher (182, 183, 184, 189, 296, 314)
44. *Geomys bursarius*—plains pocket gopher (189)
F. Heteromyidae
45. *Perognathus fasciatus*—olive-backed pocket mouse (163)
46. *Perognathus flavescens*—plains pocket mouse (42)
47. *Perognathus flavus*—silky pocket mouse
48. *Perognathus parvus*—great basin pocket mouse
49. *Perognathus hispidus*—hispid pocket mouse
50. *Dipodomys ordi*—Ord kangaroo rat
F. Castoridae—Beavers

51. *Castor canadensis*—beaver (50, 51, 137, 248, 249, 299, 305)

F. Cricetidae

52. *Reithrodontomys montanus*—plains harvest mouse
53. *Reithrodontomys megalotis*—western harvest mouse
54. *Peromyscus crinitus*—canyon mouse (292)
55. *Peromyscus maniculatus*—deer mouse (1, 40, 45, 67, 82, 116, 164, 165, 190, 231, 233, 235, 290, 312, 313)
56. *Peromyscus leucopus*—white-footed mouse
57. *Peromyscus truei*—piñon mouse
58. *Peromyscus difficilis*—rock mouse (53)
59. *Onychomys leucogaster*—northern grasshopper mouse
60. *Neotoma cinerea*—bushy-tailed woodrat (133, 154, 219, 239)
61. *Clethrionomys gapperi*—Gapper red-backed vole (45, 313)
62. *Phenacomys intermedius*—heather vole (45, 240, 313)
63. *Microtus pennsylvanicus*—meadow vole (20, 62, 229)
64. *Microtus montanus*—montane vole (19, 45, 243, 252, 253, 254, 255, 256, 259)
65. *Microtus longicaudus*—long-tailed vole (45, 313)
66. *Arvicola richardsoni*—Richardson vole
67. *Microtus ochrogastor*—prairie vole (257)
68. *Lagurus curtatus*—sagebrush vole
69. *Ondatra zibethicus*—muskrat (176)

F. Muridae

70. *Rattus norvegicus*—norway rat
71. *Mus musculus*—house mouse

F. Zapodidae—Jumping Mice

72. *Zapus hudsonius*—meadow jumping mouse
73. *Zapus princeps*—western jumping mouse (44, 45, 46, 61, 68, 238, 313)

F. Erethizontidae—Porcupines

74. *Erethizon dorsatum*—porcupine (298)

O. Carnivora

F. Canidae—Canids

75. *Canis latrans*—Coyote (52, 87, 120, 204, 227, 236, 260, 283)
76. *Canis lupus*—gray wolf (25, 47, 73, 129)
77. *Vulpes vulpes*—red fox (125)
78. *Vulpes velox*—swift fox
79. *Urocyon cinereoargenteus*—gray fox

F. Ursidae—Bears

80. *Ursus americanus*—black bear (31, 32, 100, 102, 158, 173, 204, 226, 262)
81. *Ursus arctos*—grizzly bear (72, 74, 75, 77, 78, 79, 80, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 101, 204, 215, 228)

F. Procyonidae—procyonids

82. *Bassariscus astutus*—ringtail (186)
83. *Procyon lotor*—raccoon (204)

F. Mustelidae—Mustelids

84. *Martes americana*—marten (23, 27, 141, 230)
85. *Martes pennanti*—fisher (27, 38, 141)
86. *Mustela erminea*—ermine (short-tailed weasel) (134)
87. *Mustela frenata*—long-tailed weasel (23)
88. *Mustela vison*—mink
89. *Mustela nigripes*—black-footed ferret (65, 69, 70, 71, 149)
90. *Gulo gulo*—wolverine
91. *Taxidea taxus*—badger (23, 117, 171, 191, 192, 195, 197, 297)
92. *Spilogale gracilis*—spotted skunk
93. *Mephitis mephitis*—striped skunk
94. *Lutro candensis*—river otter

F. Felidae—Cats

95. *Felis concolor*—mountain lion
96. *Lynx lynx*—lynx (147)
97. *Lynx rufus*—bobcat (103, 104, 105, 204, 214, 260)

O. Artiodactyla

F. Cervidae—Deer

98. *Cervus elaphus*—elk (wapiti) (2, 4, 5, 6, 7, 8, 9, 10, 15, 31, 36, 76, 77, 83, 93, 115, 122, 138, 140, 167, 169, 174, 200, 204, 205, 210, 221, 232, 234, 237, 258, 261, 267, 268, 270, 275, 280, 301)
99. *Odocoileus hemionus*—mule deer (83, 135, 138, 180, 199, 204, 225, 294, 295, 306)
100. *Odocoileus virginianus*—white-tailed deer (83, 204, 276, 315)
101. *Alces alces*—moose (10, 11, 12, 13, 14, 15, 16, 17, 18, 33, 108, 109, 110, 124, 148, 155, 156, 157, 209, 210, 211, 212, 272)

F. Antilocapridae—Pronghorn

102. *Antilocapra americana*—pronghorn (antelope) (26, 27, 119, 138, 160, 204, 207, 224, 244, 265, 269, 291, 295, 301, 302, 308)

F. Bovidae—Bovids

103. *Bison bison*—bison (buffalo) (81, 130, 138, 204, 208, 213, 241)
104. *Oreamnos americanus*—mountain goat
105. *Ovis canadensis*—bighorn sheep (mountain sheep) (86, 107, 128, 138, 139, 152, 206, 222, 263, 316)

General Subjects

1G. Mammals general (3, 88, 162, 188, 193, 223, 242, 251, 264, 282, 284, 285, 293, 307)
2G. Mammalian predators (106, 274)
3G. Soricidae (43, 64, 118, 136, 151, 161)
4G. *Myotis* (127)
5G. Leporidae (204)
6G. Rodentia general (201, 202, 203, 289)
7G. Sciuridae (144)
7Ga. *Eutamias* (142, 309, 311)
7Gb. *Spermophilus* (159)
8G. Geomyidae (145)
9G. Heteromyidae (134)
10G. Cricetidae (63)
10Ga. *Microtus* (126)
10Gb. *Jeromyscus* (289, 290)
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12G. Mustelidae (143, 146)
13G. Cervidae (179)
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15G. Wildlife Diseases (153)
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Estimates of Vascular Plant Primary Production in a West Coast Saltmarsh-Estuary Ecosystem

Abstract

Vascular plant primary production studies were undertaken in six Coos Bay, Oregon, salt marshes differing in plant associations, substrate, period of inundation, and degree of human interference. In each marsh, monthly samples were taken along permanent transect lines to determine aerial and root standing crop values. Estimation of death due to shedding and herbivory were included when assessing primary production values. Salt marshes with a predominance of giant bulrush, *Scirpus validus*, showed the greatest productivity (1200 G/M^2/year); disturbed marshes showed least productivity (400 G/M^2/year). Salt marshes with a predominance of *Carex lyngbei* and *Distichlis spicata* showed high intermediate characteristics (1081 G/M^2/year). Root standing crop values appear quite large (20,000 G/M^2). Further study needs to be undertaken in order to determine the importance of this plant material to estuarine food chains.

Introduction

Salt marshes are important components of estuarine ecosystems, playing a critical role in providing organic detrital material to estuarine food webs (Fenchal, 1969; Newell, 1965). They serve as a breeding ground and nesting site for many species of fish and wildlife (Hoffnagle *et al*, 1976), as settling basins for silt and organic material as well as pollutants of marine, terrestrial, and freshwater origin, and as stopover areas for many species of migratory birds (Magwire, 1976).

Salt marshes have received considerable attention on the North American Atlantic coast where low energy coastlines and barrier beaches create conditions which favor formation of extensive salt marsh systems. On the Pacific coast, however, due to the high energy nature of the coastline, salt marshes are restricted to estuaries and sheltered bays (Chapman, 1960). Little research has been done on these ecosystems. Notable exceptions include the work of MacDonald (1969) on the mollusk assemblages of the entire Pacific coast, and the work of Jefferson (1974) concerning plant community structure on the Oregon coast.

In this paper vascular plant primary production in the salt marshes of the Coos Bay estuary is assessed as a first step toward measuring organic detrital influx into the estuary.

Site Description

The Coos Bay estuary is located in southwestern Oregon 165 km north of the California border. It is approximately 5799 ha in extent, the largest estuary wholly within the state of Oregon (Akins and Jefferson, 1973).

The climate is mild, mid-latitude marine with warm summers and wet, cool winters. Average rainfall ranges from 125 cm on the coast to 250 cm at the headwaters of the Millicomma River, some 40 km inland (Oregon State Water Board, 1963). Little rain

falls from June through September. Temperatures are moderate, averaging 7°C in January and 15°C in July.

Six study marshes were selected within the estuary for primary production studies on the basis of their plant communities, salinity, substrate, and degree of human interference (Figure 1, Table 1). Plant communities were classified according to the scheme of Jefferson (1972). The South Slough marsh was selected because of its location near the upland end of the South Slough Estuarine Preserve. The site is virtually undisturbed; adjacent uplands were logged near the turn of the century and used since as low-intensity dairy farms. The Henry Metcalf Estuarine Preserve marsh is a low, marine salt marsh near the ocean entrance to Coos Bay, with an unusual diversity of plant species. Twenty species of plants inhabit the marsh from its highest to its lowest reaches. Pony Slough marsh is located adjacent to the North Bend Airport. It is within a state bird sanctuary and is an important stopover for migrating waterfowl during winter storm tides. North Slough is a long, north-south running marsh following the edge of Highway 101 north of North Bend. The study site was located in a pure *Scirpus validus* stand, a species which tolerates salt water concentrations as low as three to five parts per thousand. The Bull Island site is a highly dissected marsh across the bay from the town of Coos Bay. This location contains the largest contiguous section of salt marsh in the estuary, unaltered in the past seventy years (Herbert Lillienthal, pers. comm.). The Coalbank Slough site is enclosed on three sides by upland and enclosed on the bayward side by a recently constructed road placed upon stone. Bay water circulation into the marsh is exclusively through a 4 ft. culvert placed underneath the roadway. The impaired circulation of this marsh gives rise to a disturbed, low-productivity condition which favors invasion of terrestrial species.

TABLE 1. Characteristics of six study marshes.

Study location	Area ha	Substrate	Elevation above zero tidal datum	Species richness	Predominant plant species in order of abundance by weight
South Slough	1.1	silt/ organic	3.5 M	9	**Carex lyngbei, Distichlis spicata, Triglochin maritima, Salicornia virginica**
Henry Metcalf Estuarine Preserve	.8	sandy	.8 M	19	**Salicornia virginica, Triglochin maritima, Distichlis spicata, Carex lyngbe, Deschampsia caespitosa**
Pony Slough	21.5	sandy	.5 M	12	**Salicornia virginica, Distichlis spicata, Deschampsia caespitosa, Triglochin maritima, Jaumea carnosa**
North Slough	14.3	organic	1.5 M	1	**Scirpus validus**
Bull Island	12.2	silt/ organic	1.75 M	11	**Carex lyngbei, Deschampsia caespitosa, Triglochin maritima, Salicornia virginica, Distichlis spicata**
Coalbank Slough	3.8	organic/ silty	2.4 M	8	**Carex lyngbei, Deschampsia caespitosa, Grindelia integrifolia, Atriplex patula, Glaux maritima**

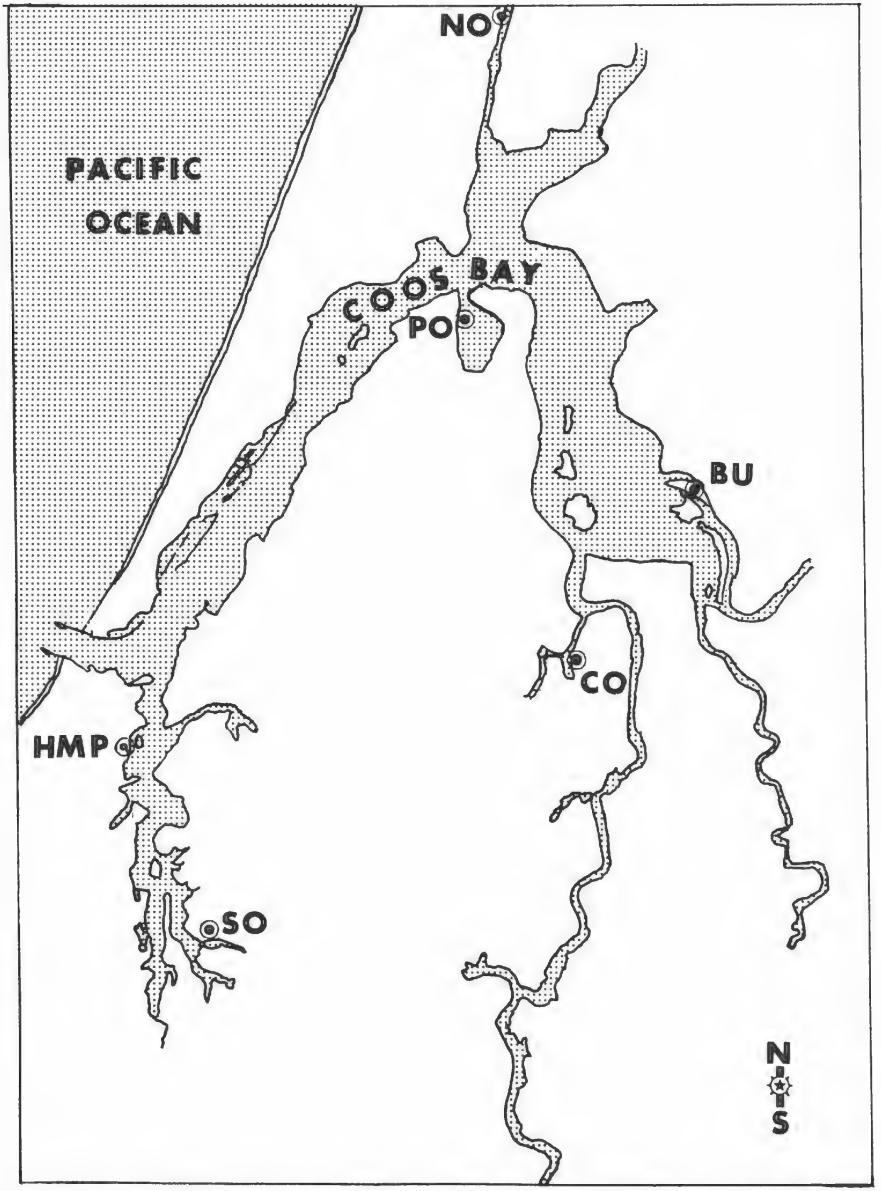

Figure 1. Coos Bay, Oregon, location of study. SO=South Slough, HMP=Henry Metcalf Estuarine Preserve, PO=Pony Slough, NO=North Slough, BU=Bull Island, CO=Coalbank Slough.

Aboveground plant production

Permanent transect lines were staked across each marsh outward from the shore. Monthly

(May-August) samples of aerial biomass were taken every 5 or 10 m along the transect line in order to obtain from fifteen to twenty-five samples from each marsh. At each sample location 1/8 sq m quadrats were laid out and all standing vegetation was clipped down to 2 cm. Each sample was bagged separately in the field and refrigerated until sorted, in order to minimize weight loss by fermentation and respiration as recommended by Boyer (1958) and Milner and Hughes (1968). Cuttings were sorted into living and dead material for each species present. Positive species identification could almost always be made. Sorted samples were then dried at 100°C to constant weight (24 hr).

The following formula (Wiegert and Evans, 1964) is used to calculate primary production from our monthly standing crop figures obtained from each marsh.

$$P_n = \sum_{n=1}^{N} (B_n - B_{n-1}) + L + P_a + G$$

where P_n = net primary production
B_n = aboveground standing crop at time n
L = losses from death and shedding
P_a = biomass added after peak accumulation
G = direct grazing due to consumers

This classic formula becomes complicated in a community of many different plant species reaching their peak biomass at different times, thus the maximum standing crop of each species in each study site has been substituted for $(B_n - B_{n-1})$, as in Eilers (1975). Eilers reasoned that in a nonwoody perennial, maximum standing crop would include only growth that had occurred during that year (excluding death due to shedding and consumption by herbivores). This alteration also in effect removes P_a (biomass added after peak biomass) since peak biomass is being measured for each species. Therefore:

$$P_n = \sum_{n=1}^{N} S + L + G$$

where S = maximum standing crop of each plant species in the study location.

A unique problem occurred in the case of *Salicornia virginica*, a woody perennial. In this case $B_n - B_{n-1}$ was resubstituted for S and April standing crop values were used as the beginning of the growing season, since at that point no green vegetation was visible.

L (the loss due to death and shedding) is calculated by assuming that the loss of dead material occurs at a constant rate throughout the year. In the early spring, before any new growth has occurred, the decrease in dead material from the past growing season is measured and projected forward linearly into the later summer months when dead material from the current growing season has begun to accumulate. This estimation of current and past dead material allows one to determine the amount of dead material attributable to the current growing season and provides an estimated value for L.

Herbivory in salt marshes is believed to be quite low, most energy being utilized as detrital material supplied to the estuary. Large herbivores are rarely present and small herbivores, primarily the deer mouse, *Peromyscus maniculata*, do not appear abundant enough to be causing significant grazing pressures on the salt marsh. Magwire (1976)

studied small mammals in the same six study locations that were used for the primary production studies, and had capture success rates of 5.7 captures per 100 trap nights. Some 80 percent of these animals captured were insectivorous shrews, *Sorex vagrans.*

Insects may be the most important herbivores in the salt marsh. In an East Coast study, Smalley (1960) established that 10 percent of the biomass (*Spartina alterniflora*) in his study area was consumed by insects. Shrag (1976), working at the Oregon Institute of Marine Biology, found that leafhoppers (Cicadellidae) feeding on *Distichlis spicata* consumed 7.27 percent of total production. Utilizing this figure, our data might be somewhat in error if greater or lesser herbivory by terrestrial arthropods is taking place.

Ash-free dry weight

Subsamples of the dryweight samples were ignited in a muffle furnace at 600°C to determine ash-free dry weight (Boyd, 1971).

Root biomass

Root biomass was sampled at each point along the transect. A 4 cm diameter core of the upper 40 cm of the marsh was obtained with a sharpened steel pipe sampler driven into the substrate. The root and soil core was extracted and removed from the pipe by insertion of a wooden ramrod. Soil cores were stored under conditions similar to aerial cuttings until processing. Soil cores were rinsed by hand over a 60-mesh-per-inch screen. A 35-mesh-per-inch screen was used for the samples originating from the Henry Metcalf Estuarine Preserve due to the coarse nature of the sandy substrate. Samples were dried to constant weight and subsamples were ashed similarly to aerial samples.

Estimates of primary production should include both above-ground and below-ground plant material. Unfortunately, it was not possible to distinguish between living and dead roots or to separate the roots by species (Schlesinger, 1977). Due to these difficulties, root biomass was not calculated, but is given, rather, in standing crop values.

Results and Discussion

Each salt marsh is a unique combination of plant species, substrate, tidal circulation, and nutrients. As a result of these variables one may expect one salt marsh to differ from another in many ways. In order to assess total primary production of salt marshes in the Coos Bay estuary ecosystem, the contribution from each representative site must be examined. Table 2 presents live and dead standing crop values for each study location during each month of the growing season. Standard deviations appear quite high due to the wide variability within each transect.

The Henry Metcalf Estuarine Preserve and Pony Slough sites both contain a high proportion of *Salicornia virginica.* On these sites the growing season begins with a good deal of "aerial" biomass already present in the form of woody non-photosynthesizing stems. Other study sites with predominately non-woody perennials show little growth at this time. As the growing season progresses, however, the *Salicornia virginica*-rich marshes, while maintaining their dominance over the lower sites, do not grow to the extent that the marshes predominated by *Carex lyngbei* and *Scirpus validus* do. The *Salicornia*-rich sites, Pony Slough and Metcalf Preserve, put on only 300 G/M^2 of aerial biomass during the growing season.

TABLE 2. Live and dead shoot standing crops for each study location during each month of the growing season.

	Marsh	April	May	June	July
Live	Metcalf Preserve	337.36 ± 320.64	442.24 ± 286.72	491.2 ± 320.8	560.24 ± 256.88
	Pony Slough	287.76 ± 123.36	324.16 ± 152.4	516.72 ± 151.2	689.12 ± 217.68
	South Slough	(63.86 ± 17.52)	571.2 ± 199.6	699.76 ± 148.	550.96 ± 183.68
	Bull Island	63.36 ± 17.52	236.72 ± 83.52	687.28 ± 196.2	596.32 ± 160.4
	North Slough	45.92 ± 24.40	204.96 ± 100.00	717.92 ± 235.04	795.36 ± 204.32
	Coalbank Slough	40.16 ± 53.13	56.96 ± 55.36	151.68 ± 153.20	205.2 ± 143.84
Dead	Metcalf Preserve	208.8 ± 166.24	162.96 ± 123.52	136.48 ± 112.42	295.28 ± 322.56
	Pony Slough	62.4 ± 92.48	35.28 ± 31.94	90.00 ± 53.12	120.08 ± 73.76
	South Slough	(106. ± 135.92)	104.00 ± 5.92	134.72 ± 133.36	126. ± 86.88
	Bull Island	106. ± 135.92	101.68 ± 108.4	283.68 ± 201.04	107.04 ± 90.32
	North Slough	316.08 ± 84.4	261.44 ± 146.00	325.12 ± 98.48	524.45 ± 119.6
	Coalbank Slough	480.16 ± 408.16	76.16 ± 67.88	98.3 ± 134.64	71.84 ± 71.92

In contrast, *Scirpus validus*-rich sites, such as North Slough, begin the growing season with stores of available nutrients and energy in roots and rhizomes. At this time they possess no live above-ground biomass. As the growing season progresses, bulrush-rich sites exhibit dramatic growth, in large part due to the nutrient and energy stores present in these roots and rhizomes. Bulrush puts on the bulk of its growth in June and July. By July, *Scirpus validus* marshes attained a standing crop of 800 G/M^2

Study sites with *Carex lyngbei* predominating possess intermediate growth rates. They grow through June, at which time their biomass declines, probably due to a temperature controlled increase in respiration or a loss of lower leaves through breakage or tidal action.

Disturbed marshes, of which Coalbank Slough site is an example, show normal but stunted growth patterns. Growth occurs well into July, but never attains an appreciable standing crop.

Figure 2 illustrates the method utilized to differentiate dead material from the current growing season and past growing seasons. Dead standing biomass is plotted for each month. As the dead biomass begin to increase near the end of the growing season, due to increased death of currently growing plants, the descending line is extended in a straight line to the month of peak dead biomass. All material underneath this line is thought to be dead material from the previous year. If the line does not intersect the perpendicular to the greatest month's dead standing crop, all material is assumed to be derived from the current growing season. In all cases except the Coalbank Slough site, in which dead material has completely decomposed, the continuation of the line does not intersect the maximum dead standing crop perpendicular.

Figure 3 separates live matter by species rather than by study site. Examination of this figure illustrates the close relationship between characteristics of marsh growth and the predominant species in a salt marsh. Well over 50 percent of the biomass in each marsh is produced by one or two species, thus sites strongly reflect the growth characteristics of the predominant species.

Primary production estimates

Table 3 presents primary production figures for each study site. These production figures integrate standing crop, litter material, and grazed material for the entire growing season.

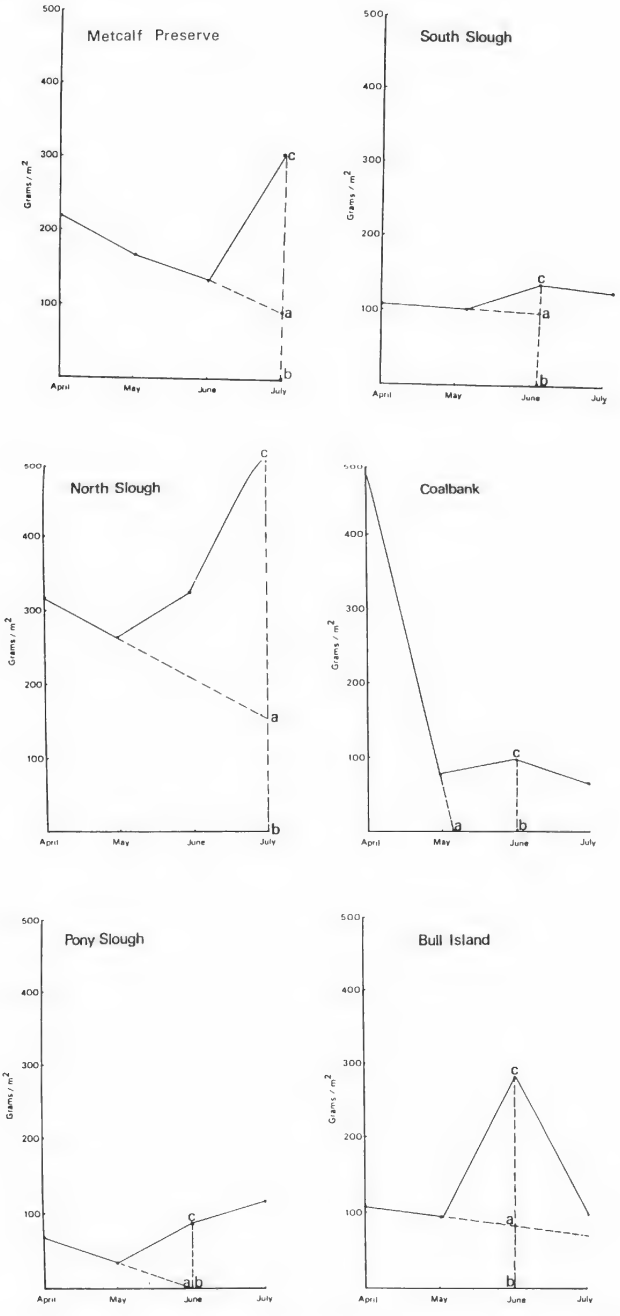

Figure 2. Changes in dead standing biomass from April to July. Estimated portion of dead shoot material (CB) derived from previous season's growth (AB).

North Slough, the bulrush-dominated stand, clearly shows the highest production over the growing season. This production, while in large part contained in the live aerial portion of the plants, is also influenced by large amounts of dead litter material lost during the growing season, perhaps due to the marsh's low tidal character. The two *Carex lyngbei* marshes, Bull Island and South Slough, which are elevated above the tide level, differ in their productivity. While comparable amounts of living material are present in each site, the amount of litter transported into the estuary during the growing

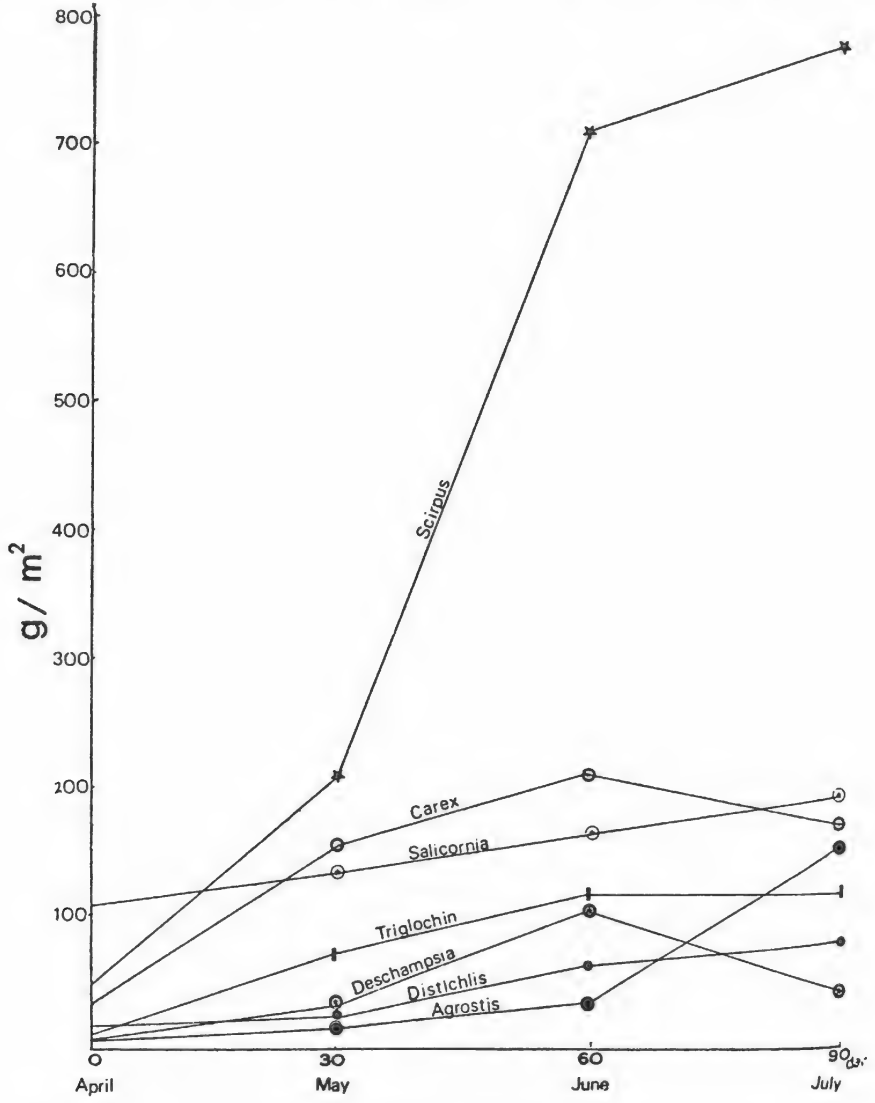

Figure 3. Biomass of seven plant species as the growing season progresses.

season seems much larger in the Bull Island site. The low marshes, Metcalf and Pony Slough, are characterized by rather low production values. Litter is relatively high for these two species, perhaps as a result of their more frequent inundation. Coalbank Slough has production values only one-third as great as those of the most productive marshes. These low values are possibly a result of restricted water circulation.

TABLE 3. Calculation of total aerial productivity for each of the study sites. S=shedding, L=litter, G=grazing.

Marsh	S	+	L	+		= Total G/M²
NO	749.4		369.4	81.7	=	1200.5
BU	815.2		192.7	73.5	=	1081.4
SO	734.8		30.0	55.8	=	820.6
PO	479.0		120.1	43.7	=	624.8
HMP	360.1		200.3	40.9	=	601.9
CO	280.6		98.3	27.7	=	406.6

Figures derived for each salt marsh community in Coos Bay compare favorably with data for other types of ecosystems shown in Table 4. Several factors unique to the estuarine environment contribute to high productivity in salt marshes. The moderating effect of ocean waters on marine climates and locally on the micro-climate of the salt marsh allows a longer growing season (Keefe, 1972). Vertical orientation of leaves in salt marsh plants reduces intense heating (Palmer, 1941), and enables the plant to expose maximum leaf surface to sunlight over the course of the day and minimizes mutual shading (Jervis, 1964).

TABLE 4. Comparison of primary productivity in different world ecosystems. Daily values for marshes based upon 200 day growing season (USDA).

Plant community From Odum (1960)	Net primary productivity G/M²/year	 G/M²/day
Wheat (areas of highest yield)	1250	3.43
Corn (world average)	412	1.13
Hay (areas of highest yield)	940	2.58
Forest (pine during years of most rapid growth)	3180	6.0
Forest (deciduous, same as pine)	1560	3.0
Spartina salt marsh (Georgia)	3300	9.0
Infertile open ocean	182	.5
Shallow inshore waters (Long Island)	1168	3.2
From Harding et al (1970)		
Eelgrass (**Zostera marini**)	4500	5.17
Immature high marsh	1087	5.43
Bulrush marsh	1201	6.00
Low sandy marsh	622	3.11

Due to the high water table in marshes, soil water is usually abundant and enriched in dissolved nutrients from the soil-water equilibrium. This high nutrient content of marsh soils and water helps maintain high productivity. As freshwater flows into the marsh, silt from upstream is trapped by marsh plants (Ranwell, 1964). In addition, the tide moves nutrients from marine sources into the salt marsh. The watery marsh environment hastens decomposition of organic matter and leads to the formation of organic colloids that absorb exchangeable ions necessary for plant growth (Keefe, 1972).

Estuary production

Assessment of vascular plant productivity in the entire estuary must consider the community level. In this analysis, different salt marsh types are grouped according to the plant species present. The extent of each marsh type present in the estuary is taken from Hoffnagle and Olson (1974). These acreages are multiplied by production figures from the preceding to obtain the total production of the estuary by vascular salt marsh plants. Using this technique, total productivity for the 7.86 x 10^6 sq m of salt marsh in the Coos Bay estuary is 7.35 x 10^9 g per year (see Table 5).

TABLE 5. Total productivity of salt marsh systems in Coos Bay based upon estimated productivity and estimated acreage.

Marsh type	Productivity (G/M^2)	x	Area (M^2) = Total
High Marsh	951	x	4.40 x 10^6 = 4.18x10^9
Low Marsh (silt and sand)	622	x	1.46 x 10^6 = 9.08x10^8
Sedge Marsh	1081.4	x	1.43 x 10^6 = 1.54x10^9
Bulrush Marsh	1200.6	x	6.06 x 10^5 = 7.27x10^8
Total			7.89 x 10^6 = 7.35x10^9
			Grams

Root standing crop and ash weight

Root dry weight and ash-free dry weight values are given in Table 6. These root standing crop values suggest two important factors operating in the salt marsh ecosystem. Total contribution of roots and rhizomes to the standing crop of the entire plant is well over 10 times that of aerial production. The sharp decline of root dry weight as the growing season progresses, and the accompanying increases in aerial growth, suggest that roots and rhizomes may function as a storehouse for aerial growth.

Root ash-free dry weights point to the important contribution made to inorganic nutrient stores by plant roots (taken here to mean both plant roots and rhizomes). At the beginning of the growing season 50 percent of the plant roots are organic and 50

TABLE 6. Dry weight and ash-weight of roots during each month of the growing season.

Marsh	April dry wt. g/m^2	April ash-free dry wt. g/m^2	May dry wt. g/m^2	May ash-free dry wt. g/m^2	June dry wt. g/m^2	June ash-free dry wt. g/m^2	July dry wt. g/m^2	July ash-free dry wt. g/m^2
Coalbank Slough	38232.08 ± 30063.38	18198.95 (47.6%)	19179.73 ± 9056.66	12213.25 (47.22%)	12213.25 ± 5390.07	8549.27 (70.%)	13375.66 ± 4697.4	11733.13 (87.72%)
North Slough	20915.38 ± 7762.66	13825.06 (66.1%)	9124.11 ± 1441.07	7517.35 (82.39%)	8877.29 ± 5206.96	7261.62 (81.8%)	6305.66 ± 2364.52	5745.9 (91.14%)
Metcalf Preserve	34474.16 ± 12133.63	10535.3 (30.56%)	11552.43 ± 4697.4	5750.79 (49.78%)	10827.91 ± 4522.24	7200.56 (66.5%)	9370.92 ± 5437.84	8905.18 (95.03%)
South Slough	No data		7205.34 ± 1950.62	4908.48 (68.12%)	5374.14 ± 3152.83	4245.57 (79.%)	7937.81 ± 3869.29	7513.13 (94.65%)
Pony Slough	12125.64 ± 6226.05	8329.1 (68.69%)	15549.2 ± 6329.55	8241.08 (53.%)	13329.49 ± 5326.39	9503.92 (71.3%)	9155.95 ± 3264.29	8419.81 (91.96%)
Bull Island	11233.95 ± 3192.6417	5028.32 (44.7)%	13853.36 ± 2794.56	5991.58 (44.%)	10748.29 ± 1291.05	8296.18 (77.%)	9554.04 ± 3821.62	9033.34 (94.55%)

percent are inorganic. By the end of the season, 90 percent is organic material. As the growing season progresses, inorganic materials are utilized and replaced by organic stores. An absolute decrease in root weight occurs during the growing season.

This paper has assessed the primary production of vascular plants in an estuarine ecosystem, taking into account death due to shedding and herbivory. Primary production and root standing crop values for five different estuarine marshes have been established. The more fundamental question concerning the fate of the photosynthetic material has not been looked at due to its complexity. It may be presumed that a large portion of the material produced in the salt marsh decomposes and enters the estuary in some form as detritus destined for further consumption by estuarine organisms (Odum and de la Cruz, 1963).

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Thomas J. Howell and Louis F. Henderson: Early Resident Botanists of the Pacific Northwest

Abstract

From the University of Oregon Library of written records over the active lives of the earliest resident plant collectors of the Pacific Northwest, the correspondence and manuscripts of Thomas Howell and Louis Henderson demonstrate well the relationships of these regional botanists with the nationally known botanists at Harvard, Chicago's Field Museum, and at Washington, D.C. The correspondence of these two field collectors of Oregon shows that in return for field collections sent to the professors and professional taxonomists, the avocational botanists of the far west were supplied with published plant descriptions and approved names for their new plant species. The records of Louis Henderson reveal a life filled with dramatic incidents.

Introduction

The University of Oregon Library has recently acquired many written records of the earliest botanists who spent most of their lives in the Pacific Northwest. These field notes, unpublished manuscripts, and letters represent active lives of field collectors within the area of the Old Oregon Territory between the years 1873 and 1939. Heretofore, they have been merely accounted for initially (Thatcher, 1976), and subsequently in more detail (Thatcher, 1978). The latter paper points out the mutual support given between these western field collectors in their geographic and professional isolation.

In the present paper I draw chiefly on the information within those manuscripts held at the University of Oregon Special Collections Library to demonstrate relationships of the self-trained plant collectors in the Pacific Northwest with their better educated and botanically more versatile correspondents of herbaria in the eastern United States. I found it desirable to view personally the correspondence of both botanists as held at the Field Museum, Chicago, in the Hunt Institute for Botanical Documentation, Pittsburgh, at the New York Botanical Garden Library, and at the Gray Herbarium Library, Harvard University.

Thomas J. Howell (1842-1912)

The Howell family arrived in 1850 over the Oregon Trail from Missouri, and settled near present Forest Grove; they moved the following year to a farm on Sauvie Island in the Columbia River near its confluence with the Willamette. That home, once dilapidated, has been restored through efforts and direction of the Oregon Historical Society, and is recognized now as a National Historic Landmark. Designated the "Bybee-Howell House," this Oregon Territorial farmstead includes over a hundred acres; it belongs to Multnomah County, and is managed in cooperation with the Oregon Historical Society. The part played by the Howell family in its history has been described by Thomas Vaughan (1974). The Howell mailing address was Arthur, Oregon, from 26 July 1880 to 30 November 1904, when the post office was closed out as a result of the extension of rural free delivery (McArthur, 1974:24).

Thomas Howell

Thomas Howell had only three months of formal education in a rural school, which accounts for his early unique spelling and faulty grammar. Through intensive self-training he overcame these handicaps to a large degree, and with the help of staunch friends, he persevered to produce the first regional flora (Howell, 1903). Powers (1935), in his *History of Oregon Literature*, states: "Thomas Howell, the grocer, learning type and printing his 800-page botany book . . . [is] the most conspicuous example of self-reliance in the field of publishing in Oregon . . . ." For lack of funds to have his book commercially printed, Howell set his own type. Lange (1955) describes the circumstances under which its seven fascicles were printed by Howell after ten years of toil (1886-1896) to produce the first manuscript draft, and the important part played by Edward L. Greene of Catholic University, Washington, D.C. in providing periodic financial support and in critically editing the manuscript, except for the absence of one significant letter, dated 17 May 1897, which is quoted here in full. In this, Greene, who had recently moved eastward after a long tenure at the University of California, Berkeley, begrudgingly offers a little financial support and scathingly criticizes Howell for alleged errors and unacceptable practices.

Washington
17 May 1897

Dear Mr. Howell:
Your note is in, also the new pages. I was wondering if your realizations from sales of your first issue could not enable you to get along for a while, without more help from me. Honestly, during this summer, I do not see how I can save any money for you. I enclose $40. but I can not spare it. It will be keeping people whom I owe out of their dues. Part iv of Flora Franciscana will soon be done. I have just had to pay down $100. on that, and there will soon be another $100. to pay there. Then an issue of Pittonia is next week to be paid for. And I am so reduced financially that I can not go even to the Rocky Mountains in vacation for sheer want of

money. I can not promise to help you to another dollar, before the end of August, or perhaps even September.

But that may be to your advantage; if you will only get a lot of copy ahead, and have it corrected until it is correct. I did not tell you, when I mentioned the *lavigatus* var. of *Ceanothus* as distinct, that it was published at the very outset as a species. I had not time to write what was needless. You have Watson's Index, and that tells the story. You did not look it up. You would not take time. So you have written *C. laevigatus* as if it were to be your species. This kind of error—born of your to (too) great hurry—will tell against your book more than you think. And errors in proof-reading, as one may charitably call them—such as *"C. pumilis"* for *C. pumilus* are so innumerable, and will so damage the book, that I shall not be surprised if reviewers either ignore your book altogether, or give it such a damning, as I warned you of before you began. They may be expected to say, in recounting even the bad spelling alone, that a great book was presumptuously undertaken by a man who could not spell; any such things, I almost expect to see if they review it at all.

Great pity I did not see either copy or proof of your Leguminous genera. There is no genus "Petalostemon"[1] it is long antedated by *Kuhnistera*, a name now in use by everyone except the Harvard gawks, whom Asa Gray, who pays them, will not let do as they please. Same of *Oxytropis*,[2] which can not stand in the place of the much older *Spiesia*. What an abbreviation for Hortus you have in your "Hor" (p. 119). Everybody else since the world began has written "Hort."!

You have one Rhamnus *masculine* gender, (Californicus), another feminine gender (Purshiana); and these things tell that your grammar ideas—that you have none! No other botanist but you has ever pig-headedly claimed his own herbarium distribution as the publication of species.[3] There never was such a rule admitted by anybody. It is everywhere condemned. Why are you so stubborn? as to write R. Howellii "P.C. Pl. Coll. 1887'? All these things tell against your book!

I have no time to look up your *Prunus villosa* proposition. The genus is *Cerasus*[4] for cherries! And with that genus name you will have no trouble with species names. I am not going to argue further about these matters. Suffice it that Britton's Illustr. Flora which will be more influential than all Gray, not only admits *Cerasus* but even *Emplectrocladus* that I reduced.

Yours,
E. L. Greene

Thomas Howell's first botanical avocation was as a horticulturist on the Sauvie Island family farmstead and his first publication in that enterprise was an 1873 list of living "plants in three and four inch pots," which he hoped to sell to gardeners and horticulturists in the Portland, Oregon, vicinity. The list is reproduced here, in part, as Figure 1. Later he printed lists of pressed herbarium specimens for sale and mailed these to his eastern correspondents. These early sales lists show evidence of his poor spelling and of a type-setting amateur.

As early as 1877 he began rather regularly to send plants for identification and first description to Asa Gray and Sereno Watson at Harvard, but at that time his spelling and grammar were so faulty that these professors probably presumed he would never provide any significant contribution to the scientific literature. Perhaps because of this assumption, Watson described Howell's first collection of the weeping spruce and named it *Picea Breweriana* (Watson, 1885), for W. H. Brewer, an early itinerant naturalist of California. Nevertheless, it was an ungracious slight to Howell, because this tree was the last of the North American coniferous trees to be discovered and described.

Within a decade thereafter Howell's knowledge of plant geography and competence as a writer seem to have advanced notably, for in *Popular Science Monthly*, there appeared

---

[1]The generic name employed by Gray and still accepted for the several species of prairie clovers.

[2]Name for the pulse family genus which includes the locoweeds.

[3]Thatcher, 1980 in *Huntia*, explains why Greene was mistaken with this accusation.

[4]The classical name for the cherry used by American taxonomist, Nathaniel Britton of Columbia University, but not by Gray of Harvard. Cerasus is still generally accepted as the specific name for one species of genus, Prunus.

HOWELL'S

Price List of Plants

FOR THE SPRING OF 1873.

I present herewith a brief list of Flowering Plants.

My stock is unusually fine and healthy this Spring, and I think you will find on comparing my prices with others, that they are lower than was ever offered in this market before.

It will be understood that these prices are for plants in three and four inch pots—larger plants will be charged for according to size.

All plants sent post paid by mail at these prices. Legal Tenders taken at par for plants by mail.

Depot—Cor. First and Oak Streets, Portland, Oregon, where samples can be seen.

I have made arrangements with Nurserymen and others so that I will be able to furnish any Trees, Plants, Shrubs, Seeds, Bulbs, etc., in this market, not named in this list.

All orders sent to T. J. HOWELL, *Portland, Oregon*, will receive prompt attention and satisfaction guaranteed.

Price Lists free on application.

DOUBLE GERANIUMS.

Maddan Lemoin—Bright rosy pink..... 50 cts.
Glorie de Nancy—Deep carmine..... 25 "
Triumph—Scarlet..... 25 "

4

HARDY HERBACEOUS BORDER PLANTS.

Crysanthemums—Large flowered.
Lucinda—Pink—white tips.
Minerva—Lilac shaded.
Pink of Pearl—Delicate pink.
Robert James—Cinnamon orange.
Miss Mary Morgan—Pink.

POMPONE, OR SMALL FLOWERED.

Aurora—Deep orange.
Aureole—Orange red.
Alex. Peel—Cinnamon.
Boul de Nirge—white—yellow center.
Innocence—Pure white.
Citronella—Deep yellow.
Antirrhinums—(Snapdragons.)
Chelome Barbata.
Dianthus Chinensis—(China pink.)
Lychnis Chalcedonica—Scarlet.
Lychnis Chalcedonica Alba—White.
Lychnis Haageana—Hybrida.
Mimulous Muschatus.
Myosotis—(Forget me not.)
Penstemons.
Pyrathorum Aureum—(Golden Feather.)
Verbena Montana.

MONTHLY ROSES.

Compt. Brobilinskil—Bright scarlet.
Hermosa—Light rose.
Souvenir de Malmaison—Very large—light flesh.
Aime Vibert—Pure white—in clusters.
Climbing Hermosa or Satina—Pink.
Gobalt—Yellow buff—very sweet.
Sombreuil—Large—creamy white.
Cels—Blush white.
Lady Warrender—Pure white.
Queen of Lombardy—Bright rose.
Sanguinea—Deep crimson.
White Daily—Creamy white.

Figure 1. Howell's work as a gardener and horticulturist came to public notice in Portland, Oregon, five years before his collections of native flora became known to Asa Gray at Harvard College.

an article by Thomas J. Howell (1883), the author obviously a resident of northern Oregon, entitled "The Geological distribution of North American forests." It seems evident that this is the same person being considered here, for library research has failed to reveal any other Oregon resident of that name who was then scientifically interested in plants. In that article he emphasizes the importance of bedrock types on the geographic distribution of the vegetation of North America; in the preparation of that paper he may have been greatly aided by Professor Thomas Condon, or by another professor of geology, perhaps one from an eastern university.

Perhaps it was this success in publication at middle age which gave him the self-confidence in plant taxonomy which is demonstrated in the following correspondence.

In a letter filed at Gray Herbarium Library, Howell assured Asa Gray that he was confident of himself on the taxonomy of the family, Portulacaceae. This letter illustrates well the often repeated statement that Howell was home-educated in English and self-taught in plant collecting and plant description. It is selected for reproduction here to demonstrate that the route of advice on matters of taxonomic description was not exclusively East to West.

Arthur, Oregon
3/28/1887

Dr. Asa Gray
Dear Friend
Your last Botanical contribution has just come to hand, pardon me for making the following criticism.

Portulacaceae

Lewisia Pursh, should be confined to the original L. rediviva or else your Calandrinia section Pachyrrhizeae should be put with it. I have studied the order Portulacaceae very thoroughly, so far as I have been able to and I find nothing to separate Lewisia from these "Calandrinias" excep the jointed scape, several sepals,/ this is broken down by "L. brachycalyx" and the accumbent cotyledons; but the jointed scape and accumbent seeds are enough, confine the genus to that and it will do, but this throws out L. brachycalyx which naturally falls into "Calandrinia."

Whatever may grow in Chili I am not able to say not having had an opertunity to study that Flora but so far as our species go your section Pachyrrhiza of Calandrinia is well marked and should have generic rank, and I will hazard the remark that a close study of the Chilean species will disclose the fact that all the species that have the capsule of our thickrooted "Calandrinias" will be to differ from Calandrinia proper fully as much as our large rooted Western ones do. Then why not put all the "Calandrinia" with this capsule in a genus by themselves and leaves the others as Calandrinia? I would arrange them as follow, (takeing your sectional name Pachyrrhiza, for a generic one without seeing wether it would be proper to do so or not).

The remainder of Howell's long protest to Gray is repetitious. Later Howell did publish in *Erythea,* "A Rearrangement of American Portulaceae" (Howell, 1893). He also corresponded with E. L. Greene and with many other botanists of the eastern U.S. in the period 1880-1895.

In 1903, Howell's *A Flora of Northwest America, Containing brief descriptions of all the known indigenous and naturalized plants growing without cultivation north of California, west of Utah, and south of British Columbia, Volume 1, Phanerogamae,* was published at last in a single bound volume of 792 pages plus 24 pages of Index. A combined collection of his seven earlier and separately printed fascicles, a very large part of the manuscript had been edited by Edward L. Greene, and it was entirely proofread by his devoted Portland friend, Martin Gorman. Howell had originally planned to publish a second volume covering the Cryptogams, but that never materialized. In spite of its flaws, his *Flora* became an excellent basis for the currently accepted floristic manuals of the region.

Louis Henderson

Louis F. Henderson (1853-1942)

The only one of the early regional plant collectors to have received an earned baccalaureate degree, Henderson was graduated in 1874 from Cornell University. He went west to teach; first he arrived in Oakland, California, then in 1875, to Oregon. From that year until 1889 he frequently collected plants with Thomas Howell. In one of his autobiographical manuscripts, Henderson expressed vividly his feeling of professional isolation:

> In all my botanical work on this coast, one thing struck me as peculiar, and yet from conversations I have had with many botanists, I find that my experience was no different from that of the average. This was the number of botanists I corresponded with for many years, and yet how few I ever met! Among these whom I regretted never meeting were Asa Gray, Sereno Watson, George Engelman, George Vasey, Frank S. Scribner, Leo Lesquereux, in America, and Renaud and Cordot in France. I have had the pleasure to meet C. P. Sargent, B. S. Robinson, M. S. Fernald, and J. M. Greenman, Harvard, and N. S. Britton at Columbia; while in Oregon I had the great pleasure to meet John Muir, Thomas Condon, C. C. Parry, C. V. Piper, and C. G. Pringle. To John Muir I listened with interest to his stories of Alaska and California, and it was at his seeing a specimen of blood-red Zauschneria in my herbarium, that he laughed and narrated for me his thrilling and well known adventure with a grizzly bear in the Upper Yosemite Valley of California. To C. C. Parry, writer, collector and delightful though modest man, I owe much for his suggestions in collecting plants. It was to C. G. Pringle, teacher in Vermont, a collector for Harvard University, and all-around good fellow and educated gentleman, that I perhaps owe most for his valuable suggestions in finding plants, mounting, and especially numbering them. I had only recently found out the importance of giving *serial numbers* to every plant I collected, save in this particular. When I had collected a plant and given it a number, I was inclined to keep to that number, no matter how often I had collected it. This, of course, often led to two similar but different plants having the same number,—a most obnoxious thing. I well remember his saying to me at my house, when he found two plants having the same number, "Remember, Mr. Henderson, there is nothing cheaper than numbers, so don't be afraid of using different numbers for not only every plant you collect, but for every time you collect the same plant,"—a lesson I have never forgotten, and which in turn I have always impressed upon my pupils and younger field men. As for the collectors who lived in our Northwestern states, I was intimately acquainted with C. V. Piper and William Suksdorf, but though I cor-

> responded and exchanged plants with John Leiberg, and William Cusick for years, I regret greatly that I never met either of them. Dear old Dr. Condon, though primarily a geologist, was as an amateur interested in botany, and many pleasant hours and delightful walks I passed in his company in Eugene and elsewhere. And to no man can the term "lovable" be used with greater propriety than when speaking of Dr. Henry Bolander. I doubt whether any collector ever added more to the knowledge of California plants than did he. But financial reverses overtook him in his favorite field of teaching in that state, and these reverses, none of his own making, but due to the unholy union of big business and politics, and he finally spent the remainder of his noble life in the private schools of Portland. Many an evening did I spend with him in his simple little home here, where with his efficient and admiring wife and the writer acting as audience, he told of his botanical wandering and discoveries in California. Also many a Sunday afternoon walk did we take to the environs of Portland, where we spent hours in his favorite pursuit,—the collection and study of mosses. On one of these occasions he told me how he "solt" Dr. Asa Gray, as he pronounced it in his German-English. The genus Bolandra was named for him, the first species being Bolandra Californica. Then Howell and I added a second to this genus in Bolandra Oregana. Shortly after, Bolander wrote Gray that he had discovered two new species of Bolandra, and named them, as I remember, Amarella and Aramintha. Dr. Gray soon wrote him in reply, "Bolander, I never heard of such rediculous specific names. Why did you do it?" At this, Dr. Bolander sent him a postal card, with the pictures of his *two young twins* thereon. A reply from Gray was characteristic, "Sold! Sold! But I know you haven't got the money." That self-forgetful, delightful, learned, and yet modest soul, Dr. R. D. Nevius, I met first when he lived in North Yakima, and about him and our trips together I hope to speak at some future time. Last, but not least, that friend of everybody and everybody's friend, M. W. Gorman, late botanist living in Portland, is perhaps remembered by many of his acquaintances better even than by me. Yet our relations were always of the pleasantest, and many an enjoyable day we spent together in your grand old Forestry Building, discussing and looking over plants.

Two more brief excerpts from a Henderson manuscript on file at the Special Collections Division, University of Oregon Library, seem appropriate here to my subject of the relationships of the early western field collectors to the establishment botanists of the recognized eastern science centers. From page 15 under the sub-heading "North Slope of North Sister, Summer 1881":

> I also found here our now well-known *Phyllodoce glanduliflora*, or sticky white heather, as we call it in English. When I sent this to Dr. Asa Gray, it was then known as *Bryanthus glanduliflorus*; and he soon wrote me in reply, "Hurrah! The first time ever known in the United States!" I may say right here, that so inadequate were our reference books to North-western flowers at that time, that practically all of the western collectors, Pringle, Howell, Cusick and the author, sent our flowers to Harvard Herbarium where the gamopetalae were reported upon by Asa Gray and the polypetalae by Dr. Sereno Watson. Slightly later we sent our Sedges to Dr. L. H. Bailey at Cornell for identification and our grasses to George Vasey, Department of Agriculture Agrostologist at Washington, D.C.

Also from Henderson's undated manuscript titled "Early experiences of a botanist in the Northwest," from its page 24 (at Mt. Adams):

> hundreds of plants were added to our collections. As Thomas Howell was supporting himself almost wholly by the sale of his collections, while I had my regular teacher's salary, I always allowed *him* to send off what collections went East for naming, as anything new, or even rare brought the most money in the plant market.

Because Henderson corresponded frequently, preserved copies, kept detailed field notebooks, and wrote autobiographical essays for his grandchildren and for oral presentation to local societies, his life as documented in the Special Collections of the University of Oregon Library appears more full of dramatic incidents than most. Elsewhere (Thatcher, 1978), I have quoted from an exchange of letters between Henderson and his long-term correspondent, Charles V. Piper (1867-1926), on file at the library at Washington State University. In that exchange it is clear that Henderson on his seventieth birthday swam the Columbia River from Hood River, Oregon, to the Washington shore. This

feat, particularly then, before the control of flow by the power dams, was notable for a person of any age.

All of his records taken together reveal a very well-organized curator, a careful, thorough field collector, and a very appealing person. Following is a series of letters from Louis F. Henderson written from Moscow, Idaho, where between 1893 and 1908 he was a faculty member at the University of Idaho. This correspondence, on file at the Field Museum, reveals a very dramatic, and to us following him, a very costly incident.

To Dr. John M. Coulter, University of Chicago,

December 29, 1905

Dear Sir:
You may be interested to know that I am offering my private herbarium for sale. The price is $2000. cash, paid when the plants are picked up and on board cars at this place. There are over 10,000 mounted sheets, consisting mostly of the plants of Oregon, Washington and Idaho.

Coulter evidently thought the Field Museum of Chicago was the more likely buyer and referred Henderson's letter to the chief taxonomist of that institution, with whom followed this exchange.

Field Museum, Chicago
Jan. 30, 1906

To Louis F. Henderson
Can not recommend its purchase. In all former purchases of mounted herbaria by this institution the price paid per sheet has not in any case exceeded ten cents. I am entirely unable to recommend the purchase of your series at double that price.

C. F. Millspaugh

To Millspaugh, Field Museum, March 16, 1906:
I have heard from three other parties that my price is too high, and I am disposed to accept this consensus of opinion. If you wish for the Field Museum my collection you can have it for $1,000. you to pay all the expenses of boxes and freight. I pack it according to your directions and see it on board cars.

On 20 March 1906 Millspaugh replied:

Can not pay until received and checked over. Can not pay boxing and cartage.

Had the transaction been completed, our knowledge of the Pacific Northwest flora and of Henderson's later life might have been greatly altered. On 30 March 1906, a fire in the administration building at the University of Idaho destroyed that herbarium and all the books, notebooks, correspondence with prominent botanists, and personal records of Professor Louis Henderson.

From the following series of letters, from Henderson to Sereno Watson, we learn about the needs of both western collectors and eastern curators; and from Henderson we confront the ethics of specimen trading.

Portland, Oregon
March 1st 1882

Mr. Watson
Dear Sir,
I received your note enclosing my lists of plants, and was much pleased to find that there were *two* new species, though from my limited botanical library, I had hoped there were more.

Iris tenuis I have seen only on *Eagle Creek*, a branch of the Clackamus River, which is itself a tributary to the Willamette River, Clackamus County, Oregon. It almost completely usurps the flat for a mile in length, and as it was but just coming into bloom when I visited the spot, I was only able to collect a few specimens. The petals and sepals are mostly white, as you found the specimen, lightly striped and blotched with light yellow and purple. Will send you more exact description later."—

Will you please inform me what auxiliary works I can find to assist me in the study of the North West flora? I, of course, have Gray's Eastern Botany, both your works on the "Botany of California", and I intend sending for "Torrey and Gray" with this mail. Will you please tell me where I can obtain your work on "North American Liliaceae". If you have any copies at your disposal, and would send me one, *with the price*, I would be much obliged to you. I believe the new Torrey and Gray is now called "Grays Synoptical Flora", am I not right? Respet yours,
471 7th ST. Portland (L. F. Henderson)

Portland, Oregon
Feb 5 '88

To S. Watson
Dear Sir,

I shall certainly be much pleased to collect Iris tenuis for you, and only wish my circumstances were such that I could altogether disregard the expense attending it, and make it a voluntary gift. You may be assured, however, that I shall make it as light as possible. Still, as the locality is entirely off the main lines of travel it will necessitate a horse for a couple of days. I shall attend to it as soon as the weather will allow me.

Since your last came to hand, the blow has fallen upon us. Though I never was personally Acquainted with Dr. Gray, yet his genial sympathy with young and unknown scientists could not but win the hearts of all his correspondents, I feel, beyond the loss to science in general, as though I had lost a personally dear acquaintance. What will the botanical world do without him? How will the Flora of North America be completed? Had his work in this direction proceeded far enough that other hands can complete it? If you have time to give my requests an answer, it will relieve a great deal of anxiety, which may however never be lessened. If *you* can at some future time send me your examination of the plants in my last bundle, beyond what you have already sent, I shall be obliged.

Yours cordially,
(L. F. Henderson)

Portland, April 9-'88

To S. Watson
Dear Sir,

I have been for Iris tenuis, have collected a good quantity of it, and hope to have it on the way tomorrow. If you receive an overwhelming box of it also from New York, I hope it will not prove superfluous. To explain. Just as I rec'd your card the other day, I re'd a *very* peculiar letter from Mr Woolson, whose contents I cannot keep (from) mentioning to you *subrosa*, but hope you will mention it to no one else. Condensing, he says: "Get me 1000 or *more* plants of I. tenuis and send *none* to anyone else and I will pay you 25 or 30 dollars(!) If you would not be willing to send me your *entire* stock, I will be willing to go in with Mr Waston, so as not to have the entire expense exceed $25.00". To this I replied, perhaps too shortly for my own good, "How do you expect me honorably to neglect the request of Mr Watson, which preceeded your(s), and send to you alone. I shall send you 1000 plants, if I have time to collect so many" (never fear about *my* exterminating it; I was from 8 to nearly 4 O'cl steadily digging at a patch 20 by 15 feet, and it is as thick as it was here for half a mile) "I will send them to you for $30.00 *c.o.d.* You to pay express. If you do not call for them in three days, I shall direct them to send the whole lot to Mr Watson." I sent off the coal-oil box full of them today, and it remains to be seen whether he will take them or turn them over to you. If he does refuse them, I shall have to call upon you for the other $7.50 of the $15.00 and saddle you with a large express bill besides. I could not plan otherwise for I was bound he should not have them for nothing after such a selfish letter.

Yours cordially
(L. F. Henderson)

Thus we learn from the ever-considerate Henderson how he handled the private interests of a commercial nursery man, which G. C. Woolson was at that time (Barnhart, 1965).

Probably it was for a once-in-a-professional lifetime opportunity to be associated with the recognized taxonomic authorities that several of our resident field collectors from the far northwest sought to live briefly in Cambridge, Massachusetts, for the Harvard experience. In truth, there were doubtlessly as many different private reasons for wishing the experience as there were regional collectors.

Louis F. Henderson and Charles V. Piper (1867-1926) spent the academic year 1899-1900 together at Harvard. Henderson was on a sabbatical leave from the Uni-

versity of Idaho and Piper on leave from the State College of Washington, Pullman. Henderson resigned at the University of Idaho in June 1908. From 1909 until late 1924 he was an orchardist in Hood River, Oregon. In 1903 or 1904 Piper became Chief Agrostologist, U.S. Bureau of Plant Industry, Washington, D.C. From that point and time he continued sporadic writing to Henderson until his own death in 1926.

The following letter from Piper's correspondence held at the University Library, Washington State University, is of interest on several counts. It indicates Henderson's interest in botanical education even while in the private business of apple-growing; in addition, his continued attention to textbook authorities and to accuracy are reflected. Chiefly, it shows again Henderson sharing himself—his happy nostalgia and in his concluding sentence some words as bitter as he ever wrote.

Hood River, Oct 22/23

My dear Professor,

——— my reason for writing you is a botanical one. I made the rather rash offer a couple of months ago, that I would make a botanical and economic collection of our wild plants for High School of this place, if the Directors would furnish merely supplies, and they took me up like a shot. Well, you know what happened to me in the fire at Idaho. It left me flat without a book, microscope to say nothing of a collection. The only books I have now, are your two floras of Washington! So first of all, do you think the Department at Washington would like a set and pay a part of only my collecting expenses which would not be much in a small county like Hood River. I suppose Mr. Coville is still at the head of the botanical department. Can you see him for me?

Then you can refer me to parties who would like to name for me the Mosses, the lichens, and especially the Fleshy Fungi (Mushrooms), in which I am now more interested than the other, on their economic side. Next, have you any second hand book-stores in Washington that deal in works on the Fleshy Fungi? Are there any new books, besides McIlvaine, Atkinson, and Miss Marshall. I must have them cheap to buy at all, for I am still in that devilish business of raising apples in which I get poorer every year, if that were possible. Well, I am now blowing out with dynamite a part of it, non-productive varieties, and that is going to give me more time for study, if not money.

If you have no good second hand book-stores in Wash. refer me to some in Boston and New York. I am going to write the Cambridge Bot. Supply Co. about books, as we are getting some of our bot. supplies there.

My wife joins me in love to you and your wife, and hope we may see you both out here sometime. Weren't those halcyon days we spent in Cambridge anyhow? The best and most profitable year I ever spent and one of the pleasantest, with our short delightful trips, all about and in Boston!

Well, if the General Gov(t) would ever do anything for the farmers besides talk in establishing the selling end of the game, we might have a little money to spend on pleasures!

Your as ever,
L. F. Henderson

The recently uncovered field notes and correspondence for Louis Henderson, Thomas Howell, William Cusick, and others at the University of Oregon invited my attention to ascertain how these records correlated with the longer-known records for these same field collectors held at Washington State University, Pullman. It became quickly apparent that the manuscript collections of both universities hold the complete correspondence of William Cusick (1842-1922) with Charles V. Piper (Washington State University, 1976). Since all of the written records of Piper and William Suksdorf, plant collector of White Salmon, Washington, had long been known to be at the university in Pullman (Weber, 1944; St. John, 1955), it was obvious that some of the correspondence of Henderson and of Howell with those two might also be available in the library of the Palouse area of the Pacific Northwest province. Until I ventured beyond the Pacific Northwest and discovered at the Field Museum the correspondence of Millspaugh with Henderson and at Gray Herbarium Library the correspondence of all the above mentioned collectors to Gray, Watson, and their successors, I did not suspect how enter-

taining a picture could be constructed for the life of any one of these early regional plant collectors. The two major deposits of written records for our regional botanists are very complementary; investigation of any deposit of written records invites the historian along still greater radii from his original point of focus. This investigation has led to the conclusion that all botanical manuscript collections should be accounted for and recorded with the National Union Catalog of Manuscripts Collections, Library of Congress, and with the Hunt Institute for Botanical Documentation, Pittsburgh, Pennsylvania. So, too, the records at the University of Oregon Library invite much further work in order to place the regional botanists featured in this paper into the entire mosaic of American botanical history.

Acknowledgments

For assistance in the retrieval of many records and for numerous personal favors I am indebted to special librarians and botanists at Ownbey Herbarium and the library of Washington State University, at the Department of Botany, Field Museum, at Hunt Institute for Botanical Documentation, at the New York Botanical Garden and particularly to the staff of the Gray Herbarium Library, Harvard University. For friendly help and exchange of information over several years, I am grateful to Terry Abraham, Library, Washington State University, to staff of the Museum of Natural History, University of Oregon, and to Martin Schmitt, Library, University of Oregon.

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Weather, Fuel, and Lightning Fires in Olympic National Park

Abstract

Seven hundred forty-seven forest fires burned 2502 ha in Olympic National Park, Washington (exclusive of the coastal strip), from 1916 to 1975. The 274 lightning fires accounted for 81 percent of the area burned; 37 fires larger than 4 ha accounted for 96 percent of the area burned by lightning fires. Lightning started fires in only 22 of the 60 years, although 3-50 thunderstorms per year occurred during the summers of a 19-year sample period. Probability of one or more fires resulting from a thunderstorm depended on the number of days without 2.5 mm of rain preceding the storm. Eighty-seven percent of the fires and all but one of the fires larger than 40 ha burned in the northeasterly half of the Park, presumably because of lower precipitation. More than half of the fires started above 1220 m elevation, and four-fifths above 915 m. Differences in fuel types and quantities had little influence on fire occurrence or behavior. Most fires started and most areas burned in the subalpine zone, which has the lightest, least continuous fuels.

Introduction

Water, not fire, is the ancient element that comes first to mind upon mention of Olympic National Park. The west side of the Olympic Peninsula in Washington is the wettest spot in the contiguous 48 states of the U.S.A. and seems, therefore, an unlikely place to study the natural role of fire. However, available weather and fire statistics reveal extensive lightning activity.

In 1976, the Pacific Northwest Region of the National Park Service contracted for a preliminary study of the fire potential within Olympic National Park.[1] This paper reports the major findings of that study.

The Park comprises about 323,890 ha of land, most of which lies as a solid block in the heart of the Olympic Mountains (Fig. 1). Elevations range from a few tens of meters above sea level to 2428 m at the crest of Mt. Olympus. Precipitation at peripheral

[1]Contract #CX-9000-6-0116. Detailed report on file at Olympic National Park Headquarters, Port Angeles, Washington, and College of Forest Resources, University of Washington, Seattle.

stations averages 2550-3680 mm annually except in the northeastern rain-shadow area, which receives as little as 760 m. July-August precipitation averages less than 5 percent of the total. Normal summer afternoon temperatures at lower elevations vary from 15 to 20°C, usually accompanied by relative humidities near 60 percent. The prevailing wind in summer blows from the west and northwest (Phillips and Donaldson, 1972).

Dense coniferous forest predominates on the two-thirds of the Park that is below

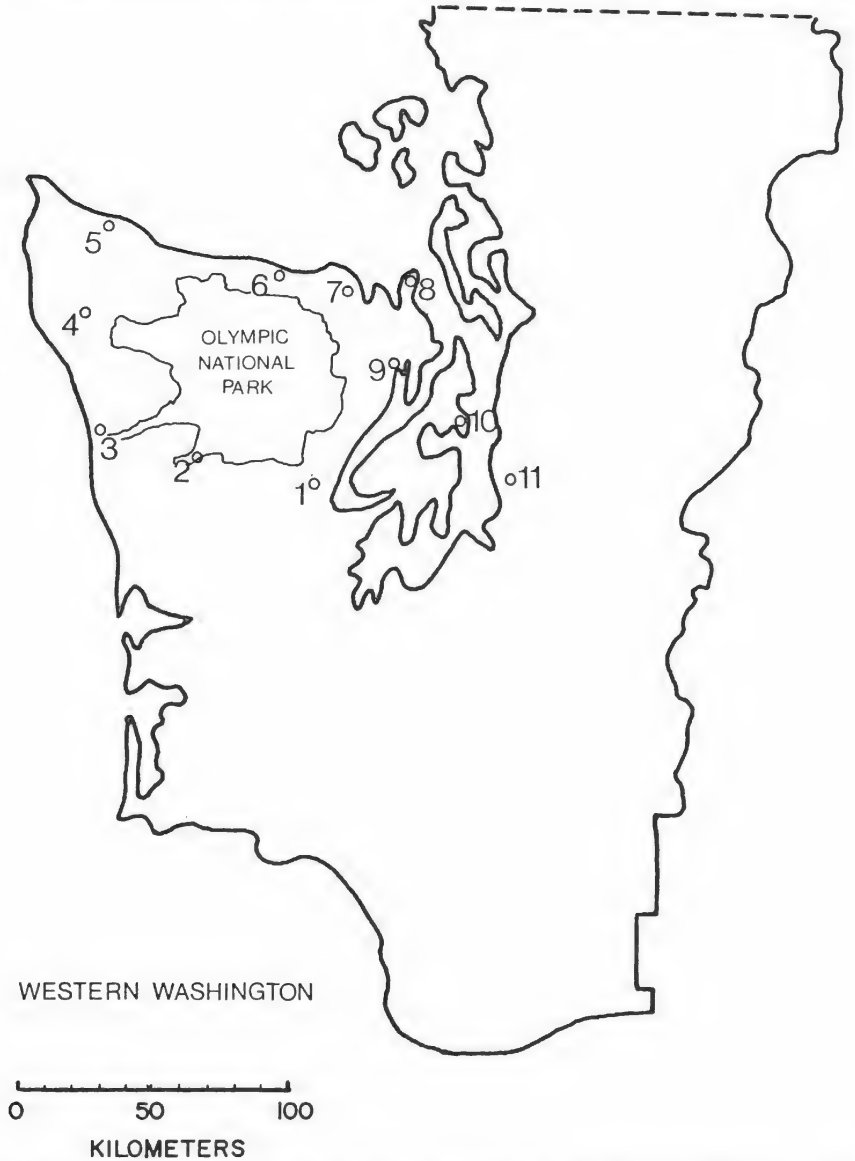

Figure 1. Location of Olympic National Park and weather stations used for references: 1. Cushman Dam; 2. Quinault R.S.; 3. Clearwater; 4. Forks; 5. Clallam Bay; 6. Port Angeles; 7. Sequim; 8. Port Townsend; 9. Quilcene; 10. Bremerton; and 11. Seattle/Sea-Tac.

timberline—generally 1670-1830 m. The main species are Douglas-fir (*Pseudotsuga menziesii* Mirb. Fromes), western and mountain hemlocks (*Tsuga heterophylla* Rap. Sarg. and *T. mertensiana* (Bong.) Carr), western redcedar (*Thuja plicata*) Donn., subalpine and Pacific silver firs *Abies lasiocarpa* (Hook.) Nutt., and *A. grandis* (Dougl. Forbes), western white and lodgepole pines (*Pinus monticola* Dougl., and *P. contorta* Dougl.), Alaska yellowcedar (*Chamaecyparis nootkatensis*) (D. Don), and red alder (*Alnus rubra*) Bong. Fonda and Bliss (1969) identified the major community types as Douglas-fir, Douglas-fir—western hemlock, western hemlock—Douglas-fir, and silver fir—western hemlock in the montane zone; and silver fir—mountain hemlock and subalpine fir in the subalpine zone.

Methods

The 1916-1975 fire history of the Park was compiled from records of the Pacific Northwest Region, U.S. Forest Service, Portland, Oregon, and from those records of Park Headquarters, Port Angeles, Washington. Information on thunderstorm occurrence came from fire lookout and weather station observations obtained by the Washington State Department of Natural Resources for the years 1945-1963. Published weather records and summaries for the same period from 11 peripheral stations (Figure 1) provided data on precipitation and wind (Phillips and Donaldson, 1972). Probability that occurrence of lightning would start one or more fires was calculated as a function of the number of rainless days since a day on which all 11 stations reported at least 2.5 mm of rain.

Surface fuels were measured by the line-intercept technique (Brown, 1974) along 10 or 15 randomly oriented transects in each of 8 stands representing 7 community types (Fonda and Bliss, 1969). At the end of each transect, duff depth was measured and converted to weight according to relations found by Balci (1964); expected initial rate of spread of surface fire and probability of crownfire occurrence (crowning potential)were determined with objective keys (Fahnestock, 1970); and fire rate of spread and resistance to control were estimated with reference to regional standards (U.S. Forest Service, 1968). Extensive reconnaisance indicated that the samples were sufficiently representative for this general study.

Fire History

The statistical record showed that 747 fires burned about 2502 ha from 1916 through 1975 (Table 1); of these, 63 percent were man-caused, but lightning fires accounted for 81 percent of the total area burned.

Man-caused fires are an annual feature; only two years (1954, 1972) had none. The maximum number in a single year (1965) was 23. Since 1946, man-caused fires have burned only about 10 ha in all, with no fire larger than 4 ha. This good record appears

TABLE 1. Summary of forest fire experience 1916-1975.

Size Class	Number of Fires			Hectares Burned		
	Man-caused	Lightning	All	Man-caused	Lightning	All
A (<.1 ha)	408	159	567	2.8	2.0	4.8
B (.1-3 ha)	47	78	125	34.0	77.3	111.3
C (3-30 ha)	16	27	43	283.0	415.8	698.8
D (30-300 ha)	2	7	9	145.7	586.2	731.9
E (>300 ha)	——	3	3	——	955.5	955.5
TOTAL	473	274	747	465.5	2,036.8	2,502.3

due to effective prevention and prompt suppression, especially in view of greatly increased visitor use.

By contrast, lightning fires occurred in less than one-third of the past 60 years (Figure 2). Six years accounted for 82 percent of all lightning fires; three years had more than 50 fires each. Ninety-four percent of the total area burned by lightning fires occurred in only four years, three of which were also high-occurrence years. Fifty-seven percent of all lightning fires burned less than 0.1 ha each; another 29 percent were smaller than 4 ha, and only 4 percent (11 fires) exceeded 40 ha. The largest fire in 1924 burned 348 ha.[2] A downward trend in maximum fire size may reflect improving fire-control capabilities and changing fire control policy. In the early days, inaccessible

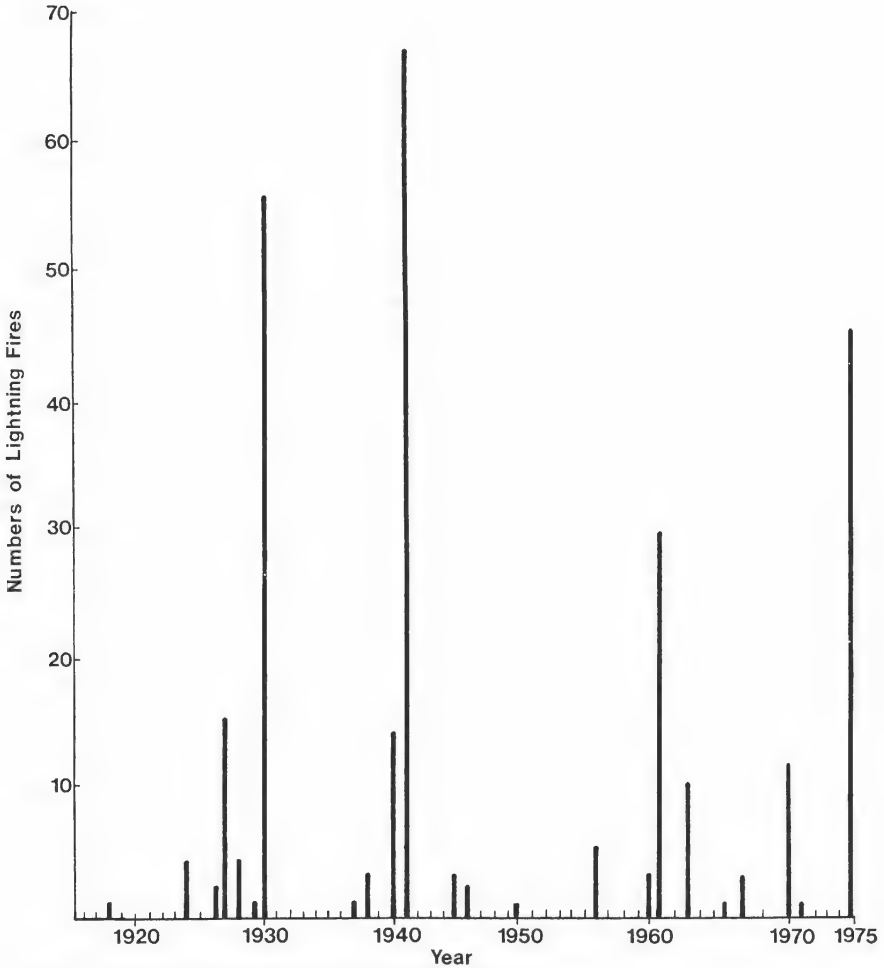

Figure 2. Annual occurrence of lightning fires, 1916-1975.

lightning fires had low suppression priority and could burn unmanned for considerable periods (William Goodpaster, Hoodsport, Washington, pers. comm.).

Extensive stands of relatively young forest containing occasional fire-scarred older trees bear witness to fires antedating the statistical records. The largest such areas are in the north and northeast part of the Park. Limited fire-scar dating placed the last fire in the Elwha at 1891 and that in Maiden Creek at 1901. Another fire had occurred about 45 years earlier in Maiden Creek, and still older scars undatable with the period of exploration and early development suggest the fires were man-caused, as others in the general area are known to have been.[3]

Some areas burned more than once, as evidenced by occasional deeply scarred trees, usually western redcedar, with the wood exposed by the first fire charred by a subsequent fire. We found one of these that had last burned more than 220 years ago, judging from the charred face. Ages of old, evenaged Douglas-fir stands were 300-plus years in several instances, suggesting that the Olympic Peninsula experienced the same fire episode that burned millions of hectares on Vancouver Island and the adjacent mainland of British Columbia (Schmidt, 1970). Although lightning probably caused most prehistoric fires in the Park, Indians may have started some, since certain tribes (e.g., Quilleute, Quinault) hunted in the interior during summer (Singh, 1966).

Fire in Relation to Environmental Factors

Weather Effects

Occurrence of Lightning

Thunderstorms generally develop in western Washington when cool, unstable, marine air is advected aloft over warm continental air. This process commonly takes place when an upper-level low lies over the region or is moving northward along the California coast. Frontal, orographic, and radiational thunderstorms also occur either independently or in conjunction with this situation (Phillips and Donaldson, 1972). From 1945 through 1963, June through September, 447 thunderstorms were reported in the Park, averaging 24 per year and ranging from 3 to 50 per year. Heaviest thunderstorm activity occurred from mid-July through mid-September, but June also had significant numbers of storms.

Occurrence of Fires

Some reported thunderstorms produce no cloud-to-ground lightning, some occur when fuels are too green or wet to burn, and some produce enough rain to extinguish part or all of the fires they start. From 1945 to 1963, for one or a combination of these reasons, lightning fires in Olympic National Park occurred only from July 6 to September 12. The percentage of storms that start fires bears a direct relation to the number of days between the storm and the last rain of at least 2.5 mm (so-called "significant rainfall") at all of the 11 weather stations (Figure 3). Fewer than one storm in five started fires within five days of a significant rain; about half the storms started fires after 15-20 dry days, but upwards of 70 percent of storms started fires after 25 dry days. On

[2]Since completion of this study, the 1978 Hoh Lake fire burned about 400 ha.

[3]Olympic National Forest file memorandum 1—INFORMATION—Olympic—Historical, of Jan. 21, 1943, by Vondis E. Miller.

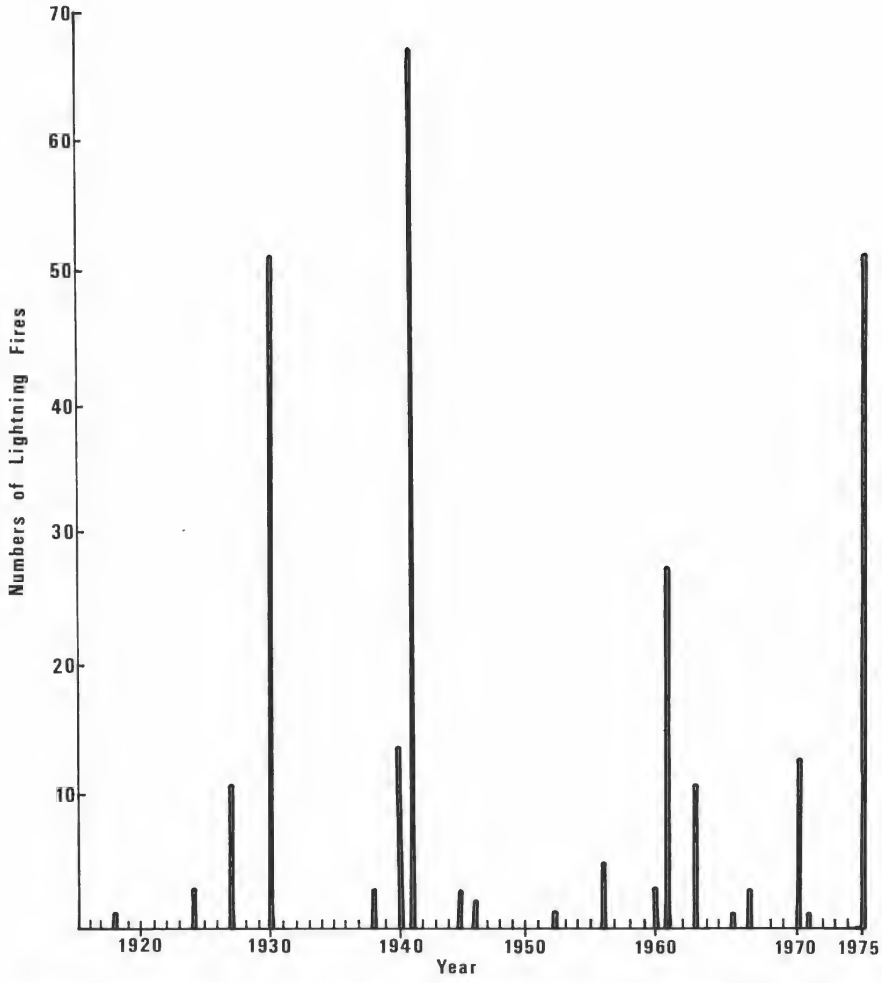

Figure 3. Proportion of thunderstorms that started fires in relation to days since 2.5 mm of rain at 11 reference weather stations, 1945-1963.

the other hand, storm occurrence and length of the antecedent drying period varied inversely. Only about 1 percent of all lightning storms occurred after 30 or more days without a significant rain. This information validates the fact that most summers are relatively moist, with only short periods between rains of more than 2.5 mm.

Occurrence of Dry Periods

Dry periods long and intense enough to let fires start and encourage their spread usually result from one of two synoptic situations, each of which produces an east-west pressure gradient accompanied by east winds west of the Cascade Range. The first situation involves the northerly movement of a thermal trough to a position along or just off the

Washington coast; the second, most common in fall and winter, involves development of high pressure east of the Cascades due to inflow of cold continental air (Cramer, 1957). The July 17, 1941 fire "bust" came at the end of the first type of situation; on September 11-12, 1961, winds produced by the second situation caused severe fire control problems on several fires which had started earlier.

Topographic Effects

Physiography

The Park can be divided logically into a western slope that includes only westward-flowing drainages and an eastern section whose streams flow north, east, and south except for the Quinault River above the mouth of O'Neill Creek. As noted earlier, the west slope receives very heavy annual rainfall, the eastern section much less. The eastern section comprises 57 percent of total area, but has had 87 percent of all lightning fires, including all but one of those larger than 40 ha (Fig. 4). The physiographic effect appears to be purely a matter of precipitation.

Elevation

Lightning fire occurrence in Olympic National Park, as in the northern Rocky Mountains (Barrows, 1951), varies with elevation. Eighty-two percent of the fires have started above 914 m and 51 percent above 1220 m. Above 1220 m, occurrence rate has been about the same (1.1/50,000 ha/yr) on both sides of the Park; at lower elevations, the eastside rate (.72/50,000 ha/yr) is about triple that of the westside (.23/50,000 ha/yr). Fires larger than 4 ha accounted for 96 percent of all burned area; 75 percent of this area resulted from ignitions above 1220 m and 91 percent from ignitions above 915 m. Only two fires that reached 40 ha started below 915 m.

Fuel Effects

A fuel-type map of the Park (in Olympic National Park Fire Atlas) as of about 1940 shows roughly 90 percent of the area as non-forest or low to moderate in both expected rate of fire spread and expected resistance to control (U.S. Forest Service, 1968). Relative numerical ratings corresponding to descriptive words are:

	Low	Moderate	High	Extreme
Rate of spread	1	5	25	125
Resistance to control	1	2	4	8

The fuel-type map, adapted from the U.S. Forest Service's 1936 "Forest Type Map for the State of Washington," shows fuel hazard in subalpine and some bottomland forest as Low-Low, in other oldgrowth as Low-Moderate, and in young forest (less than 100 years old) as mostly Moderate-Moderate, with some areas of Moderate-Low and Moderate-High. A few thousand hectares of recent burn, in scattered patches, have higher ratings due to the presence of standing and fallen fire-killed trees. The old map still gives a generally valid picture of fuel hazard in the Park.

Surface fuel loading tends to be light (<112 tonne/ha) in subalpine community types and moderate (112-224 tonne/ha) in montane types that have been undisturbed for a long time (Table 2, Figs. 5, 6). Expected rate of spread is low to moderate according to U.S. Forest Service (1968) standards and never more than 12 (usually much lower) on the 100-point scale of an objective key (Fahnestock, 1970). Resistance to control is generally low to moderate. Probability of crownfire is moderate to high

TABLE 2. Dead fuels and fuel ratings in relation to habitat type.[1]

Community Type[2]	Woody Surface			Forest Floor[3]	Total Surface Fuel	Snags	Fuel Rating[4]			
							By Key[5]		R-6	Standard
	<7.6 cm	>7.6 cm	All				R/S	C/P	R/S	R/C
	tonne/ha					no./ha				
Subalpine types:										
LP	6.1	53.6	59.7	26.9	86.6	27	2	7	Mod.	Low
AF	6.3	53.4	59.7	28.7	88.4	16	7	6	Low	Mod.
MH-SF	4.7	16.4	21.1	23.5	44.6	3	1	3	Low	Mod.
Montane types:										
DF (Sa)	6.9	61.0	67.9	43.7	111.6	2	4	2	Low	Mod.
DF (He)	9.6	26.2	35.8	57.2	93.0	2	4	3	Low	Low
DF (Bu)	6.3	64.8	71.1	37.0	108.1	40	2	4	Low	Mod.
DF-WH	9.0	82.3	91.3	57.2	148.5	8	1	2	Low	Mod.
WH-DF	15.9	119.9	135.8	60.5	196.3	5	4	3	Low	Mod.
WH-DF (Bu)	9.6	216.8	226.4	168.1	394.5	9	7	4	Mod.	High

[1]According to Fonda and Bliss (1969).

[2]AF=Subalpine fir; DF=Douglas-fir; LP=Lodgepole pine; MH=mt. hemlock; SF=Pacific silver fir; WH=western hemlock; (Bu)=1917 burn; (He)=herbaceous understory; (Sa)=salal understory.

[3]On the basis of 13 tonne/ha per cm of depth (Balci, 1964).

[4]R/S=rate of spread; R/C=resistance to control; C/P=crowning potential.

[5]On a relative scale of 0-100 for R/S and 0-10 for C/P (Fahnestock, 1970).

[6]On descriptive levels of Low, Moderate, High, and Extreme (USDA Forest Service, 1968).

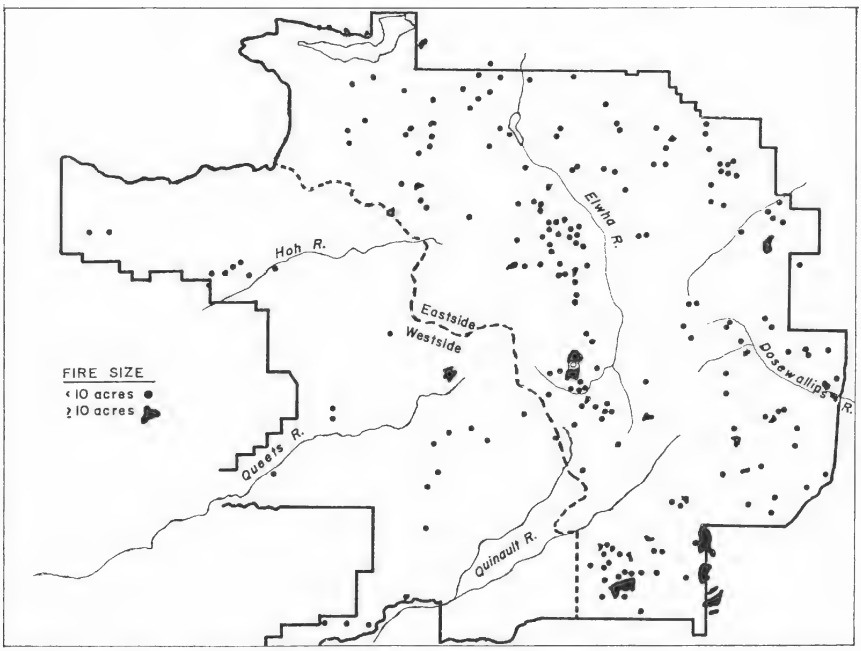

Figure 4. Lightning fire locations and area burned in Olympic National Park, 1916-1975.

(3-7) in the subalpine zone, low to moderate (2-4) elsewhere. Crown fuel is abundant but relatively unlikely to ignite initially because of wide separation from surface fuel. A 59-year-old burn (man-caused) in montane forest (Table 2) had by far the heaviest dead-fuel loading and the highest fuel-type rating (Moderate-High). The worst fuels seen (but not measured) rated Extreme-Extreme, and were in a previous winter's blowdown just east of the Elwha River above Elkhorn Guard Stations (Fig. 6d). Occurrence

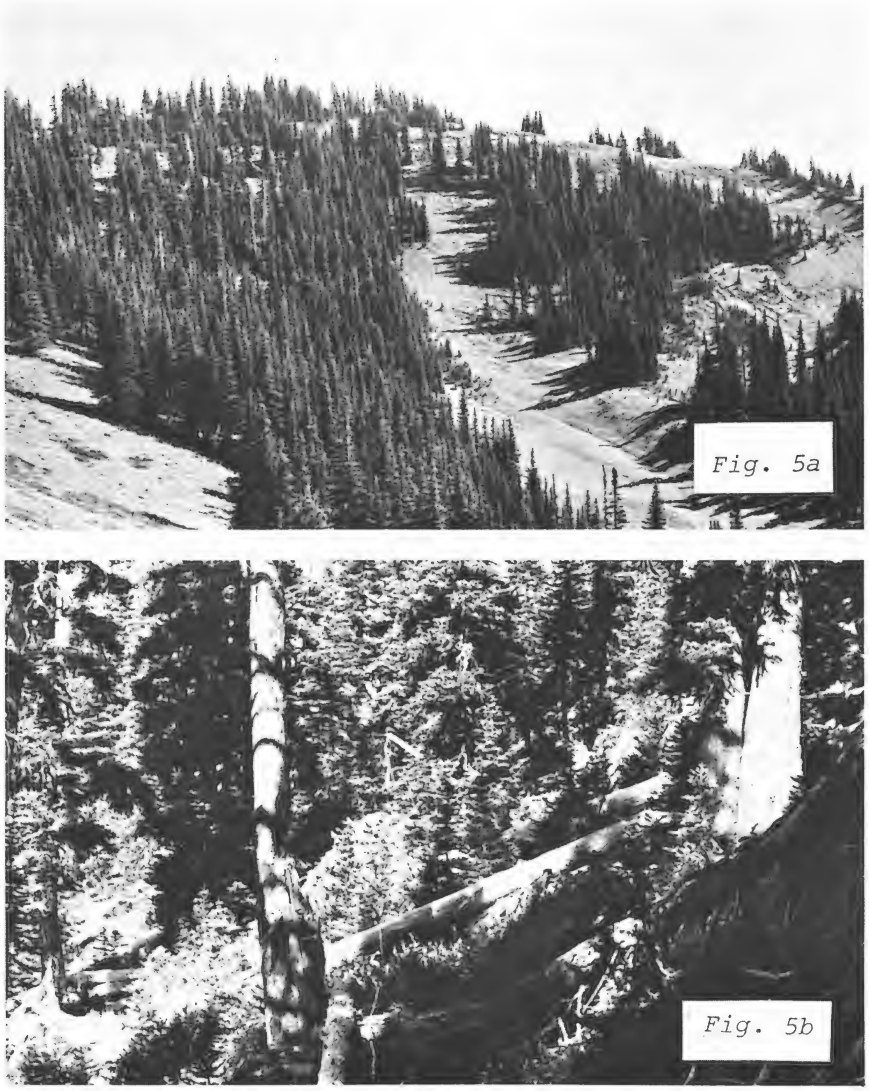

Figure 5. Forest and fuels of the subalpine zone; a. General view, showing discontinuity that tends to limit fire spread; b. View in the very common oldgrowth subalpine fir type with typically patchy fuel.

of older blowdowns nearby emphasized the known effect of occasional high winds as a cause of high fuel hazards.

Fuel types for the east side of the park can be redefined somewhat to incorporate a few refinements based on the present study. The entire subalpine zone is rated as Low-Low. (Some of the old burns technically still may have higher hazard, but they are too small and scattered to be of consequence.) Both oldgrowth and younger montane forest is Low-Moderate. However, separate mapping of the two age-classes appears desirable because they present somewhat different suppression problems: bigger wood to cut in the oldgrowth, higher probability of crowning in the young forest. Oldgrowth is also divisible into Douglas-fir and other species because of variation in resistance to control from very low in the herbaceous-understory (Fig. 6b) to high in the salal phase (Fig. 6c) (Fonda and Bliss, 1969). The "non-commercial rocky" classification on the 1936 forest type should be rated Low-High: fires spread slowly in the sparse fuel, but are hard to control because of rough terrain and rocky soil.

Fire Impact

Lightning fires of the past 60 years in Olympic National Park have had negligible impact, in terms of area burned. At the present rate, nearly ten thousand years would be required for the whole Park to burn over once. As noted earlier, however, there is ample evidence of much more extensive burning before the period of record. In any case, impact is a matter of what fire does to an ecosystem, not just how much area it covers.

A variant of the catastrophic fire regime prevails in the Park, as in other moist conifer forests made up of short-needled species (Fahnestock, 1976). That is to say, fires of appreciable size tend to occur at long intervals, kill a large proportion of the trees, and leave more fuel, consisting of fire-killed trees, than existed before. The subalpine situation fits the picture especially well: the fires of the twentieth century there are highly visible from the air because large living trees have been virtually eliminated, but dead trees are conspicuous, both standing and down. Similarly, the sharp edges and evenaged expanse of some relatively young stands appear to show the outlines of older fires rather precisely. However, low elevation burns in old growth can be hard to identify from the air. Mortality may be limited to thin-barked, sub-canopy species—hemlocks, true fir, some redcedar—leaving a nearly continuous high cover of Douglas-fir and big cedar crowns; e.g., the 1938 burn traversed by the Lake Constance Trail.

The really significant fact of fire impact in the Park is that burned areas are reforested quickly and completely. The extensive young-growth areas became established within a decade of the fires that gave rise to them, and the stands are denser than a timber-management forester would want, often of the "dog-hair" type. Young trees are less prominent and stands sparser at high elevations, but this situation is to be expected because slow development and spotty distribution are characteristic of subalpine forest. Thus, the qualitative impact of fire is to revise general age-class structure and species composition, not to cause prolonged denudation.

Summary and Conclusions

Lightning-caused forest fire is a significant natural process in Olympic National Park. From 1916 to 1975, one year in three has had at least one fire, one in six has had 10 or more; appreciable area burned one year in 15. Nevertheless, the net fire impact was

Fig. 6a

Fig. 6b

Figure 6. Forest and fuels of the montane zone: a. Typical Douglas-fir—western hemlock type; b. Herbaceous phase of Douglas-fir type; c. Salal (*Galtheria shalon*) phase of Douglas fir type; d. Recent blowdown in the Douglas-fir—western hemlock type.

negligible during the period: 2502 ha burned, but no fire was larger than 348 ha. Fire-scarred trees and extensive evenaged stands are evidence of big fires at long intervals. The most recent of these (late 1800s) may have been man-caused; earlier big fires probably resulted from lightning. During the period of record, man's activities have been responsible for nearly twice as many fires but only one fifth as much burned area as lightning.

Over and above the production of lightning, weather is the main determinant of when fires occur and how much area burns. The probability of a lightning fire occurring depends on elapsed time since a rain of at least 2.5 mm, ranging from less than 30 percent after eight dry days to >70 percent after 28 days. Long dry periods are associated with easterly flow produced by well-understood and rather predictable synoptic weather situations.

Topography largely determines where fires start and are most likely to become large. About 87 percent of lightning fires have started in the drier east side of the Park. More than half of the fires and 75 percent of the burned area occurred above 1220 m.

Fuel hazard is low to moderate over most of the Park; high-hazard areas are scattered and relatively small. The subalpine zone has the lowest hazard but the greatest number of fires and area burned.

The current exploratory study is hardly sufficient basis for sweeping conclusions or firm management decisions, but it has some strong implications and indicates direction for future research:

(1). Over rather long time periods, the impact of uncontrolled lightning fires would be tolerable throughout most of the Park because of small extent and rapid recovery of burned areas;

(2). To the extent that fire protection is considered necessary, weather forecasts and simple precipitation records can be used to direct the effort and minimize cost;

(3). Fuels are not a critical variable governing ignition and spread of lightning fires. Sufficient fuel exists practically everywhere to support fire spread; but hazard ratings are mostly low to moderate, with too little contrast to affect management decisions significantly. However, high-hazard fuels in heavy visitor-use areas are a factor to reckon with in protection from man-caused fires; and

(4). Fire history investigations in selected areas of the Park should be undertaken to provide better understanding of the periodicity of major fires. Climatic history should be studied concurrently, as feasible, to find out how long-term weather fluctuations affect fire periodicity.

Acknowledgments

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The Genus Saussurea (Asteraceae—Cynareae) in Montana

Abstract

Previously only a single species of *Saussurea* had been reported from Montana. Recently two additional species were discovered, requiring a reappraisal of the status of the genus in the state. In this report, taxonomic treatment and distribution data for the Montana taxa are presented.

Introduction

Saussurea is a circumpolar genus of more than 100 arctic and alpine species. The center of distribution of the genus is in Eurasia, but approximately five of the species are distributed in North America. Three taxa are distributed in the conterminous United States. While most investigators have listed none for Montana (Rydberg, 1900; Standley, 1921; Booth and Wright, 1959), Hitchcock *et al.* (1969), and Hitchcock and Cronquist (1973) have reported one species, *S. americana* D. C. Eaton, for the state. The junior author, however, has recently discovered two additional species, *S. densa* (Hook.) Rydb. and *S. weberi* Hultén, here. The purpose of this report is to provide an account of the genus as it is now known from Montana.

Taxonomy and Distribution

Saussurea DC.

Perennial herbs with erect stems and watery sap; leaves alternate, cauline, margins entire or dentate to pinnatifid; heads discoid, arranged in dense, corymbose or capitate clusters at the stem apex; flowers perfect, regular, violet-purple, blue, or rarely white; receptacle flat or convex, naked or bristly; phyllaries in 3 or more series, tightly to loosely imbricated; styles with a ring of hairs beneath the stigmatic branches; anthers caudate; achenes somewhat compressed, striate; pappus in two series, the outer of short, barbellate bristles, the inner of longer, plumose bristles, the inner bristles deciduous as a unit.

Key to the Species

1. Stems 3 to 12 dm long; leaves broad, ovate to cordate, margins sharply and evenly toothed ..... *S. americana*
1. Stems 0.5 to 2 dm long; leaves narrow, elliptic to lanceolate, margins entire or irregularly toothed
   2. Outer phyllaries scarcely imbricated, narrow, lanceolate, with acuminate to attenuate apices ..... *S. densa*
   2. Outer phyllaries well imbricated, broad, ovate, with obtuse apices ..... *S. weberi*

Saussurea americana D. C. Eaton, Bot. Gaz. 6:283. 1881.

Theodorea americana Kuntze, Rev. Gen. 1:368. 1891.

S. alpina var. *cordata* Kurtz., Engl. Bot. Jahrb. 19:354. 1894.

Large perennial herbs with stems 3 to 12 dm long; herbage arachnoid-tomentose becoming glabrate; leaves petiolate to subsessile, ovate to cordate, lower leaves 9 to 20 cm long, 4 to 7 cm wide, gradually reduced upwards, margins denate with well developed, evenly spaced teeth; outer phyllaries broad, ovate, arachnoid-tomentose, apices acute to acuminate; florets purple, rarely white; flowering in August and September.

Distribution: *Saussurea americana* is the most common member of the genus in Montana. The plants are found in the more western mountain ranges of the state (see Fig. 1) at 1600 m to 2400 m elevation. The taxon occurs in moist calcareous or granitic soils in subalpine meadows, on slopes with northern or eastern exposure, and along stream banks. The species grows under full or partial insolation in a diverse flora including (among many others) *Senecio triangularis*, *Delphinium occidentale*, and *Osmorhiza occidentalis*.

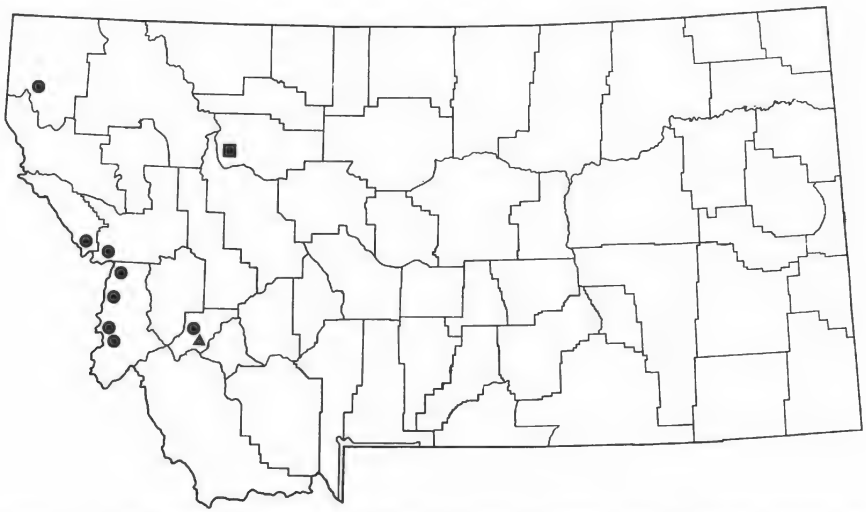

Figure 1. Distribution of *S. americana* (circles), *S. densa* (triangle), and *S. weberi* (square) in Montana.

Saussurea densa (Hook.) Rydb., Bull. Torrey Bot. Club 37:541. 1910.

S. alpina var. *densa* Hook., Fl. Bor.-Am. 1:303. 1834.

S. nuda var. *densa* Hultén, Fl. Alaska and Yukon 10:1627. 1950.

Dwarf perennial herbs with stems 0.5 to 1.5 dm long; herbage glabrate to arachnoid-villose; leaves petiolate to subsessile, narrowly elliptic to lanceolate, lower leaves 4 to 12 cm long, 1 to 2 cm wide, gradually reduced upward, margins entire or with irregularly spaced teeth; outer phyllaries narrow, lanceolate, arachnoid-villose, apices attenuate to acuminate; florets purple; flowering in July and August.

Distribution: *Saussurea densa* is known only from one locality in the Lewis and Clark National Forest in Teton County (see Fig. 1). Here the taxon occurs at 2450 m on steep, well drained, northwestern slopes under full insolation. The plants grow scattered in small, calcareous soil pockets in talus rockslides with *Claytonia megarhiza*, *Androsace lehmanniana*, *Saxifraga oppositifolia*, *Stellaria americana*, and *Mertensia viridis*.

Saussurea weberi Hultén, Sv. Bot. Tidskr. 53:202. 1959.
Dwarf perennial herbs with stems 0.8 to 2 dm long; herbage arachnoid-floccose; leaves petiolate to subsessile, ellliptic to lanceolate, lower leaves 3 to 8 cm long, 0.8 to 2 cm wide, gradually reduced upward, margins entire or with a few poorly developed teeth; outer phyllaries broad, ovate, villous, apices obtuse; florets purple; flowering in July and August.

Distribution: *Saussurea weberi* is known in Montana only from Mount Tiny and adjacent Goat Flats of the Anaconda-Pintlar Mountains in Deerlodge County (See Fig. 1). The only other populations of this species are in central Colorado. In Montana, the taxon occurs at 2850 m in moderately dry alpine meadows and adjacent slopes of northwestern exposure. It grows in well developed, calcareous soils derived from the Newland Limestone formation under full insolation. The species is associated with *Poa alpina*, *Carex scirpoidea* car. *pseudoscirpoidea*, *Agropyron caninum* var. *latiglume*, and *Senecio lugens*.

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Determinants of Mineral Lick Utilization by Feral Horses

Abstract

Feral horses in the Alberta foothills visited both naturally occurring mineral licks and salt grounds established for cattle, ingesting quantities of soil at both lick types. All age and sex classes of animals were involved in lick use. Analysis of soil samples revealed that water-soluble Na occurred at consistently higher levels within as compared to immediately outside the licks. Soil Na levels in artificial licks were replenished over the summer as were levels of water-soluble K, Ca, and Mg. Sodium levels in cured forage were low; it was postulated that Na deficiency thus constituted the basis for year-round lick use, an apparent peak in spring being due to increased excretory loss of Na. Benefits other than sodium supplementation possibly derived from lick use are discussed.

Introduction

Ingestion of soil by wild herbivores at natural mineral or salt licks is a well documented and widespread phenomenon. Varying degrees of lick use have been reported for a diversity of species, including the majority of North American ungulates (Cowan and Brink, 1949). Early investigations into the chemical composition of lick material (Rush, 1932; Dixon, 1939; Beath, 1942; Cowan and Brink, 1949) failed to identify an underlying and widely applicable explanation for the utilization of these areas; but more recent studies (Stockstar *et al.*, 1953; Dalke *et al.*, 1965, Knight and Mudge, 1967) have strongly implicated sodium as the major element sought. Despite the apparent biologic importance of these lick areas, there have been few studies relating their utilization to the ecology of individual species (Hebert and Cowan, 1971; Weeks and Kirkpatrick, 1976). Objectives of the present study were to determine the chemical composition of lick soils utilized by feral horses in the Alberta foothills, and to examine factors influencing seasonal variation in lick use.

Study Area

The study area encompassed approximately 200 km^2 of foothill terrain directly west of Sundre, Alberta (51° 35′ N, 115° 5′ W). The area is underlain primarily by sandstone, siltstone, and mudstone, with shale, conglomerate, coal, and bentonite forming minor components (Ollerenshaw, 1966). Soil-forming parent materials consist of glacial tills, alluvium, colluvium, lacustrine deposits and organic materials (MacKenzie-Grieve, 1970). Soils belonging to the Luvisolic, Brunisolic, Regosolic, Chernozemic, Gleysolic, and Organic Orders were mapped within a small part of the study area by Beke (1969), but within the area as a whole Luvisolic, Organic, and Chernozemic soils predominate. Vegetation cover is a mosaic of forest and meadow communities.

Natural mineral licks occur throughout the area in mesic valley bottoms characterized by sedge (*Carex* spp.), low, open shrub (*Salix* spp./*Betula glandulosa*) cover, and hummocky microtopography. Water saturation for at least part of the year appears to be a requisite characteristic, and many licks are associated with groundwater discharge areas. Development of the licks appears to be due primarily to large herbivore activity—vegetation is chewed away from the sides of and between the hummocks, and denuded areas develop as the animals eat and trample the soil. Size varies from a few m^2 to over 5000 m^2. Some of the larger licks are virtually denuded and appear on aerial photographs taken in 1972, indicating long-term utilization. A number of artificial salting grounds developed for cattle also are located within the study area.

Methods

Licks were located and observations on their use were made during June-August 1975 and January-December 1976. Observations of animals and animal signs within licks were made in conjunction with other field work and were therefore largely opportunistic in nature; however, examination of licks for sign of recent use spanned all seasons.

Five natural and three artificial licks were chosen for soil sampling in mid-June 1976. At four of the natural licks, soil samples were taken from five denuded hummock faces and composited into a single sample, as were five subsamples from bare areas between the hummocks. The fifth site lacked hummocks and samples were obtained only from flat areas. At the artificial licks, between two and five subsamples were obtained from areas in which the soil had recently been chewed or licked away. At both lick types, soil subsamples also were obtained along each of the four cardinal compass lines at a distance of 5 m outside the rim of the lick crater, and were composited into a single "outside" sample. Subsamples were obtained from the first 5-10 cm of the soil profile at all sampling locations. Additional within lick soil samples were obtained from a fourth artificial lick in September 1976, and from the three original artificial licks in November. All samples were air-dried immediately after collection and were ground to pass a 2 mm sieve. Weight loss upon ignition at 600°C for 1 h provided an estimate of soil organic matter. Mineral soils were subjected to particle size analysis (Bouyoucos or hydrometer method). pH was determined on a soil-water paste using a pH meter. Electrical conductivity of duplicate 1:5 soil:water extracts was determined with a Model 31 YSI Conductivity Bridge, and water-soluble Na, K, Ca, and Mg were determined on the same duplicate extracts by atomic absorption spectrophotometry (Black, 1965). Phosphorus was extracted in duplicate with dilute $NH_4F + H_2SO_4$ (Robertson, 1962) and measured colorimetrically through the use of ascorbic acid reductant.

Fifty fresh horse fecal samples were collected each month during 1976 and stored frozen in plastic bags. Prior to analysis they were composited into monthly samples on an approximately equal dry weight basis, oven-dried at 55°C for 48 h, then ground to pass a 1.5 mm mesh. Vegetation samples were obtained during late October 1976 from six different meadow sites, all of which were grazed to some extent by horses. Sites were chosen to represent the range of available meadow habitats.[1] At each site an ungrazed stand was selected and a 15 m transect was established within the stand. Herbaceous vegetation was clipped to ground level and collected from five 2 x 10 dm plots placed

[1]Major gramineous plants were *Agropyron subsecundum*, *Carex aquatilis*, *C. rostrata*, *Danthonia intermedia*, *Deschampsia caespitosa* and *Festuca scabrella*.

at random along the transect line. Litter was removed from the plots before clipping. After oven-drying at 55°C for 48 h, the individual plot samples were composited into a single sample for each site. The fecal and vegetation samples were analyzed for total P, Na, K, Ca, and Mg at the Alberta Soil and Feed Testing Laboratory, Edmonton.

Results

Site Utilization

Feral horses utilized licks for a variety of activities, including soil-eating, rolling, resting, play, and social interaction. Direct observations of animals and an increased occurrence of sign suggested a peak in soil ingestion at both lick types during April-June, a period of increased mineral loss in the feces (Fig. 1). Soil ingestion also occurred during winter (November-February), however. During the period of snow cover, horses removed soil from hummock sides in the natural licks; access to soil in artificial licks was gained by pawing away overlying snow up to 30 cm in depth. Artificial licks were used by horses during summer and fall, but there was no evidence of soil ingestion at natural sites during these periods—even though they were used for other activities.

Movements of herds toward licks were direct. Horses visited licks at various times of day and for periods of varying length. Four instances of soil-eating at natural licks were all less than 10 min in length, but at least one was interrupted when the animal became aware of the observer's presence and left the area. Undisturbed periods of soil-eating at artificial licks lasted up to 40 min and possibly longer, as some observations had to be terminated due to darkness.

Over one-fourth of the total population of horses (58/206) were observed eating soil at licks. That this high a proportion was observed during non-systematic observations indicates the likelihood that most, if not all, of the population were involved in utilization of these areas. All sex and age classes were represented in the observed sample.

Soil Characteristics at Natural Licks

All natural licks chosen for sampling were developed on bottomland soils with high organic matter content (Fig. 2). There were no consistent trends in organic matter content among hummock, flat, or outside lick samples.

Only Na occurred at consistently higher levels within than outside the licks (Table 1). Although levels of P, K, Ca, and Mg were each higher within than outside in one or more licks, there was no consistent pattern, as was the case with Na. When concentrations were expressed on an equivalent weight basis, Na was highest in all licks, comprising between 55 and 80 percent of the total water-soluble cations at each site.

Soil Characteristics at Artificial Licks

Artificial licks were located on well-drained, upland mineral soils. Organic matter content was variable but there were no apparent differences among spring, fall, and outside levels (Fig. 3). All samples were medium-textured with the clay and silt fractions together generally predominating.

Sodium levels in late spring were consistently higher within than outside the artificial licks (Table 2). Although within lick values were highly variable, as might be expected from their presumed dependence on the presence of salt during the previous

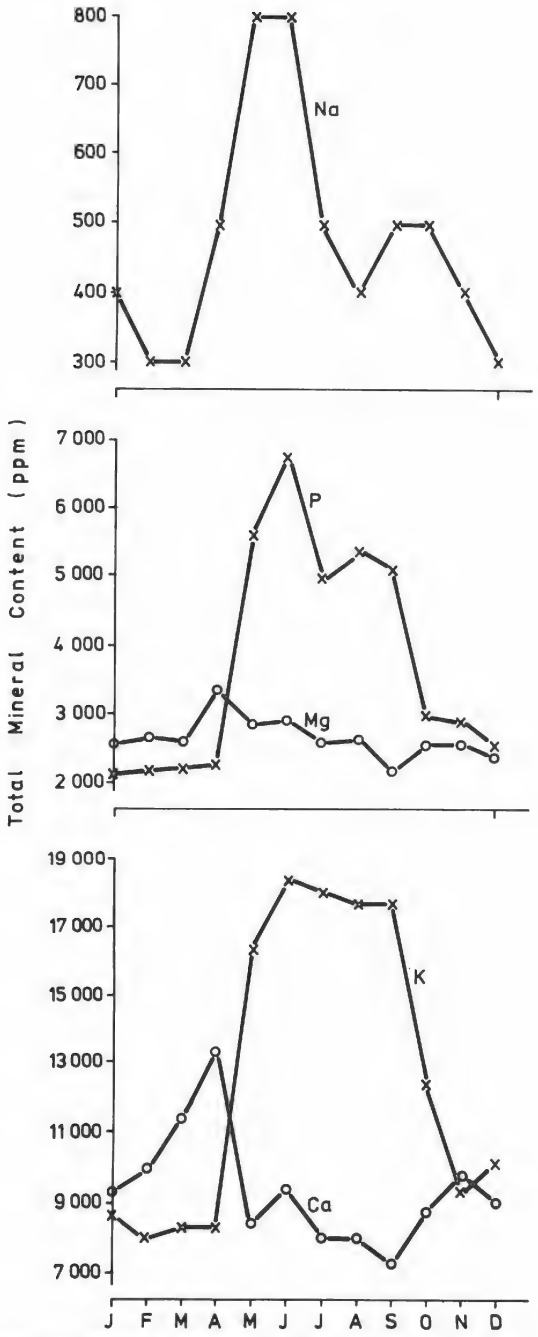

Figure 1. Monthly variation in mineral content of horse feces.

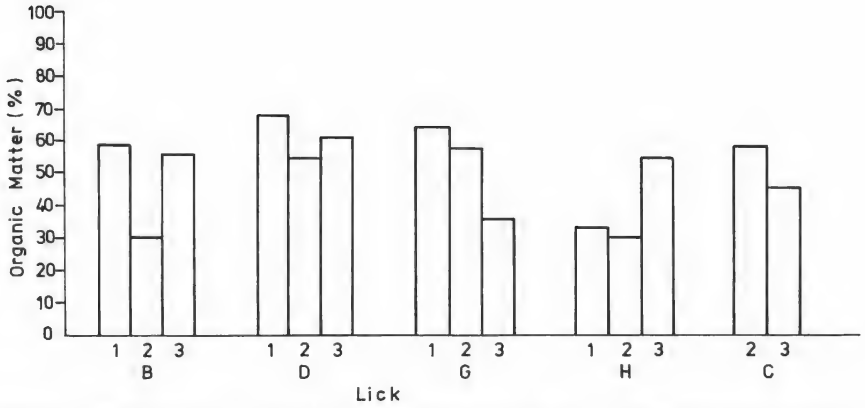

Figure 2. Organic matter content of soil samples from natural licks. 1=within lick (hummocks), 2=within lick (flat), 3=outside lick.

summer, outside levels were very similar among licks. Fall Na values increased over spring values in two or three cases, indicating a recharging of Na levels over the summer. Again, however, within lick values were highly variable among licks. The value for Lick 1, included for comparative purposes, confirms the high Na levels that may be reached in fall. In contrast, Na levels in cured forage were low (Table 3)—generally much lower than soil Na levels found within licks. This difference is likely magnified when it is considered that total Na was measured in vegetation, whereas the values for the licks represent only water-soluble Na.

TABLE 1. pH, electrical conductivity, and mineral levels in soil samples from natural licks.

Site	Sample origin	pH	E.C.[1]	Mineral levels (ppm) P	Na	K	Ca	Mg
B	outside lick	7.0	6.4	4	38	6	108	23
	within lick (hummocks)	7.9	8.8	8	185	7	88	23
	within lick (flat)	8.0	8.1	5	190	5	81	13
D	outside lick	6.5	3.8	6	75	3	34	7
	within lick (hummocks)	8.2	10.3	3	290	3	91	12
	within lick (flat)	8.4	8.4	21	245	3	36	8
G	outside lick	6.5	2.7	9	55	1	27	3
	within lick (hummocks)	7.8	7.6	1	200	1	38	6
	within lick (flat)	8.2	9.9	7	265	7	77	9
H	outside lick	7.1	4.2	7	59	8	52	16
	within lick (hummocks)	8.2	6.3	1	210	2	35	6
	within lick (flat)	7.6	4.7	2	140	2	23	4
C	outside lick	7.6	4.4	7	81	2	77	9
	within lick (flat)	8.7	13.5	20	435	11	102	21

[1]Mmhos/cm x 10^2

Levels of K, Ca, and Mg in licks followed a pattern similar to Na, being higher within than outside during spring in two of three cases, and increasing over summer and into

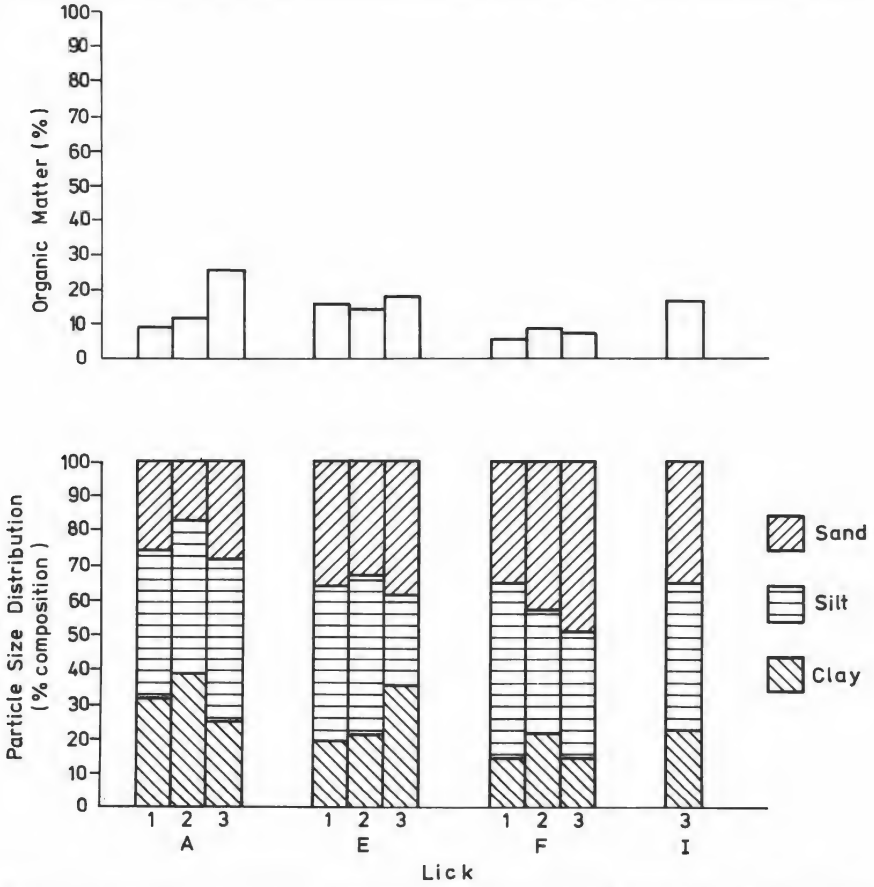

Figure 3. Organic matter content and particle size distribution of soil samples from artificial licks. 1=within lick (spring), 2=outside lick (spring), 3=within lick (fall).

TABLE 2. pH, electrical conductivity and mineral levels in soil samples from artificial licks.

Site	Sample origin	pH	E.C.[1]	Mineral levels (ppm) P	Na	K	Ca	Mg
A	outside lick	6.7	1.1	81	19	10	10	2
	within lick (June)	5.9	24	188	540	70	25	5
	within lick (Nov.)	6.8	36	155	750	118	29	9
E	outside lick	6.4	1.9	555	25	22	16	3
	within lick (June)	5.9	21	90	410	44	76	15
	within lick (Nov.)	6.0	22	39	405	67	80	22
F	outside lick	7.8	2.1	70	24	21	21	3
	within lick (June)	8.7	2.9	11	77	12	14	1
	within lick (Nov.)	8.1	96	140	2230	272	120	30
I	within lick (Sept.)	7.6	48	229	1070	237	65	16

[1]Mmhos/cm x 10^2

fall. At all of the licks within, levels of K, Ca, and Mg were higher in fall than were outside levels. The values for Lick 1 confirm the high fall levels of K, Ca, and Mg that can be reached, probably from excretory products of the large numbers of animals using these sites.

TABLE 3. Total mineral levels in herbage from meadow communities, October, 1976.

% dry matter	P	Na	K	Ca	Mg
Mean (n=6)	0.14	0.03[1]	0.60	1.14	0.20
S.D.	0.04	0.01	0.23	0.30	0.04

[1]Equivalent to 300 ppm.

Discussion

If it is correct to hypothesize that horses ingested soil for its mineral content and that the same element was sought in both types of licks, P and K would be eliminated from consideration due to generally low levels in natural licks. Ca and Mg would also be eliminated, as they were not consistently found at higher levels within than outside the natural licks (this argument could also be used to eliminate P and K). Only Na was found at elevated levels within both lick types. Thus, from soil chemical composition data, Na (and/or some other elements not included in the analysis) would appear to be the major constituent sought. This conclusion is consistent with those of recent studies concerned with sodium dynamics (Hebert and Cowan, 1971; Weir, 1973; Weeks and Kirkpatrick, 1976), although Na may not be present at concentrated levels within all licks (Henshaw and Ayeni, 1971; Botkin *et al.*, 1973).

From documentation of Na levels in forage, body fluids, excreta, and mineral licks, Hebert and Cowan (1971) and Weeks and Kirkpatrick (1976) argued that sodium stress experienced by mountain goats and white-tailed deer in spring was countered by lick use. Weeks and Kirkpatrick (1976) postulated that Na loss was related to peak obligatory intake (and subsequent excretion) of K and H_2O in food. Similar evidence indicates that in the Alberta foothills feral horses experienced Na loss in spring and may likewise have ingested sodium-rich soil as a supplementary source. Other electrolytes also were lost, but their concentrations within lick soils relative to concentrations in forage did not suggest replacement through lick use. Trapping with salt is an effective means of capturing feral horses in this area in spring (R. Logan, pers. comm.), attesting to the development of strong sodium hunger during this season.

Herbaceous vegetation available to horses was low in sodium; mean content of cured forage was only .03 percent, similar to the level at which domestic sheep are unable to maintain salt balance (Jones *et al.*, 1967). The low level of Na available in forage is consistent with observations of use of both natural and artificial licks (in combination) throughout the year, peak use in spring apparently coinciding with a peak in sodium stress. Sodium was the only element found at consistently higher levels within than outside both lick types, and it reached substantial levels over the summer in at least three of the artificial licks studied. Salt is normally included in domestic horse rations because "the commonly used feeds do not contain sufficient sodium to meet body needs" (Maynard and Loosli, 1969). Thus, the conclusion that horses might seek supplementary Na throughout the year seems justified.

The sudden influx of Na (both in block and loose salt form, and incorporated with

soil) in artificial licks during the summer may also explain the apparent lack of natural lick use by feral horses during this period. It is noteworthy that utilization of natural licks by domestic pack horses in the Alberta foothills ceases when the animals are offered block salt (R. Logan, pers. comm.). Further evidence for the attractiveness of salt to horses is provided by an observation by Dobie (1952) on one of the old methods of capturing mustangs. He notes that "woodsmen learned that the solution from a rain-soaked sack of salt hung in a tree would bring wild horses . . . to lick the ground beneath." This study documents the fact that Na becomes concentrated at the soil surface of artificial licks and is attractive to horses. Sodium levels in these licks probably decrease over winter as the Na-impregnated soil is consumed (Na levels at cattle salt licks in spring were similar to those found in natural sites); thus, the use of natural licks during winter and spring was probably related to both availability (reduced snow depths on hummocks and softening by sun exposure) and the decrease in Na levels at the artificial salting grounds.

Although the analytical data are consistent with Na-related utilization of both types of licks, elements not included in the analyses must also be considered. Because I, Co, and Cl were constituents of the salt put out for cattle, they would be expected to follow the same pattern of increase from spring to fall documented for Na. Sulfur is excreted via both the feces and urine (Maynard and Loosli, 1969), and may also have become concentrated near the surface in artificial licks. From indirect evidence it appears unlikely, however, that any of these elements would constitute the primary attraction in either lick type. Symptoms of iodine deficiency are rare in mature horses (NRC, 1973), dietary sources apparently being sufficient to meet requirements. Horses also have a very low cobalt requirement, remaining healthy on pastures on which ruminants have died from cobalt deficiency (NRC, 1973). Cowan and Brink (1949) ruled out cobalt as an attraction in natural licks in western Canada because it was found in less than half of their samples. Chlorine was present in all samples analyzed by Cowan and Brink, but it occurred in very small amounts and was no more abundant in lick soils than in non-lick soils, leading them to conclude that it was not the element sought. Although some inorganic sulfur can be utilized by non-ruminants, and has been reported in natural licks by other investigators,[2] it is not known to be an essential dietary constituent for horses (NRC, 1973).

Benefits other than Na supplementation may also accrue from lick use. For instance, the suggestion by Shaposhnikov (1953) that ingestion of fine textured soil may aid digestive regulation is consistent with an apparent peak in lick use in spring, when horse feces became amorphous and electrolyte loss increased. The addition of certain clay minerals (zeolites) to non-ruminant rations is believed both to improve digestive efficiency and control diarrhetic diseases such as scours (Mumpton and Fishman, 1977). Diarrhea in domestic horses is treated with fine materials such as kaolin and chalk, which form protective coatings on the mucous membrane of the intestine (Rossdale and Wreford, 1974), thus presumably decreasing fecal water loss. Soils within artificial licks were medium textured (clay and silt fractions predominating) while those in natural licks were organic (of small particle size), but whether ingestion of these soils had any influence on water content of fecal material is unknown.

[2]A major study of the occurrence of sulfur in North American mineral licks is being conducted at the University of Illinois. Total sulfur in lick D was reported as 3147 ppm in a sample from hummock faces and 1900 ppm in a sample from flat areas.

Soil ingestion by feral equids occurs in a variety of environmental settings in North America, but it is unclear whether it fulfills a common function. Feral horses were observed eating organic soils (Welsh, 1975) on Sable Island off the coast of Nova Scotia, but Na levels were not determined. Horses also were observed lapping at salt-water foam on the beach, and were presumed to have been using this to supplement mineral requirements "in the same way other mammals use a salt lick." Feist and McCullough (1976) in a study in Montana-Wyoming observed a lone stallion eating "mud of a dark gray color from a nearly dried up water puddle" in spring, suggesting that horses may obtain minerals in this manner. They also offered an observation of domestic horses eating mineral soil from a newly ploughed field in Canada. Feral burros (*Equus asinus*) in California spent approximately 10-20 min every three days eating salt-encrusted soil beneath saltcedars in riparian habitat (Woodward and Ohmart, 1976). However, none of these studies documented mineral levels in ingested soils, nor did they comment on social behavior associated with lick use. Social factors may be important determinants of lick use in other species (Knight and Mudge, 1967) and certainly occurred during the present study in the form of agonistic interactions and play, and possibly social facilitation of soil-eating. Maintenance functions (rolling, shade-seeking) also occurred in some licks but were secondary to soil ingestion and attendant Na supplementation—the apparent primary determinants of lick use.

Acknowledgments

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Pacific Silver Fir in the Coast Range of Southwestern Washington

Abstract

Abies amabilis occurs on the summit of prominent ridges and peaks from 1200 to 2800 ft elevation and at the head of major drainages in the Coast Range of Southwestern Washington.

Discussion

The distribution of Pacific silver fir (*Abies amabilis*) in the Coast Range of southwestern Washington is not well known. Range maps fail to show the occurrence of this species in the Coast Range south of the Olympic Mountains (Little, 1971). Other references state that Pacific silver fir in Washington is found on the west slopes of the Cascades and in the Olympic Mountains, but omit mention of this species in the Coast Range of southwestern Washington (Fowells, 1965; Franklin and Dyrness, 1973; Hitchcock *et al.*, 1969).

Pacific silver fir is found in the Willapa Hills of Wahkiakum, Pacific, and Lewis Counties, the Doty Hills of Lewis County, and the Black Hills of Thurston County. Northwest of the Doty Hills, it is found in the vicinity of Pack Sack in Pacific County, and on Blue Mountain and Minot Peak in Grays Harbor County. This species occurs on the summit of prominent ridges and peaks from 1200 to 2800 ft elevation and at the head of major drainages, but is absent from the summit and immediate slopes of Boistfort Peak, at 3110 ft elevation, the highest point in the Willapa Hills. Locations where Pacific silver fir is found receive over 60 in annual precipitation and during the summer are frequently covered by low clouds that extend inland from the nearby Pacific Ocean; these clouds help maintain a cooler, moister climate than that found in the adjacent lowlands.

Pacific silver fir in this region is commonly associated with western hemlock (*Tsuga heterophylla*). Less common associates are Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) and an occasional Sitka spruce (*Picea sitchensis*). Understory vegetation is similar to that described for the *Abies amabilis* Zone in the northern Oregon Coast Range and in the Olympic Mountains (Franklin and Dyrness, 1973).

Most mature stands of Pacific silver fir in the Coast Range of southwestern Washington have been harvested. Although many of the clearcut areas have regenerated with other conifers, immature Pacific silver fir can be found.

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Freshwater Bivalve Molluscs and Southern Plateau Prehistory: A Discussion and Description of Three Genera

Abstract

Review of analyses of bivalve molluscan remains recovered from archaeological sites in the Columbia Basin reveals several potentially rewarding lines of research. Molluscan faunas may indicate prehistoric changes in stream regimes suggesting environmental changes, or may indicate shifting subsistence strategies. Description of three bivalve genera commonly used as food by prehistoric peoples are presented to facilitate identification, and ecological data are summarized to aid interpretation of shells recovered from archaeological sites.

Introduction

Identification and analysis of molluscan faunas recovered from archaeological sites in the Columbia Basin (or Southern Plateau culture area) has yet to become a regular practice. This scholarly neglect is attributable to two major factors: 1) a general lack of comparative materials, and 2) only three genera of pelecypod or bivalve were used as dietary adjuncts by prehistoric peoples. Everyone working in the area quickly learns these things, and apparently assumes little further information can be derived from bivalve remains. The first factor will be addressed in the form of presentation of criteria for distinguishing the shells of the different taxa. The second factor will be approached in a review of the use and potentialities of bivalve mollusc analysis in studies of Southern Plateau prehistory.

Taxonomy

Henderson (1929) originally listed 18 species of bivalves for the Columbia Basin. Burch (1972, 1973) lists 20 species of freshwater bivalves for the state of Washington, and his more recent terminology will be followed here. The freshwater bivalves of Washington are listed in Table 1. Note that apparently only *Margaratifera*, *Gonidea*, and *Anodonta* were regularly exploited by prehistoric peoples. The smaller sphaeriacean clams (pea, pill, and fingernail clams) were apparently not a significant resource and are seldom recovered by usual excavation techniques.

Bivalves in Prehistory: A Review

Enbysk (1956) discusses shells from Lind Coulee (Fig. 1), and documents the presence of 15 taxa, mostly gastropods (snails), from various localities in the coulee. Three bivalve taxa are represented: *Anodonta*, *Pisidium*, and *Sphaerium*. Taylor (1960) produced a list of six gastropods recovered from the Roadcut Site (35WS4) near The Dalles, Oregon. Drake (1963) reported the bivalve *Margaritifera*, two genera of terrestrial gastropods, and one genus of freshwater gastropod from archaeological sites in the Camas Prairie

region of Idaho. Samples from various sites in the Round Butte area of Central Oregon included one genus of gastropod and *Margaritifera* (Roscoe, 1967). Roscoe presents an excellent discussion of *Margaritifera* ecology often cited by Southern Plateau archaeologists in this report (see also Rosco and Redelings, 1964). Nelson (1969) notes the presence of "freshwater mussels" at the Sunset Creek Site (45KT28) near Vantage, Washington. Grabert (1970) briefly mentions that both *Margaritifera* sp. and *Gonidea angulata* were recovered from sites in the Okanogan River Valley of North-central Washington and Southern British Columbia. "Shellfish use is [indicated at] numerous sites south of the International boundary" while less frequently north of the boundary (Grabert, 1970: 230). Shellfish utilization seems to have intensified from *ca.* 7000 B.P. (Before Present) to A.D. 1850 in the Lower Okanogan Valley (Grabert, 1970: 264-272). Dunnell and Campbell (1977: 65) indicate that only *Anodonta* was represented in the mollusc remains recovered from sites on Hamilton Island. These types of qualitative statements are of limited value in most studies of archaeological faunal remains. Quantitative analyses often permit more complete and in-depth interpretations (see for example Grayson, 1977; and Smith, 1975): they are highly recommended in future studies of archaeological remains of molluscs.

Data from the Vantage Region (Swanson, 1962) suggested a change from only *Margaritifera falcata* to *M. falcata* and *Gonidea angulata* through time (Table 2). Swanson's (1962: 24) statement that "the presence of *angulata* in a site may prove to be useful in establishing a relative chronology" is an indication of the potentialities of bivalve analysis in studies of human prehistory.

Leonhardy and Rice (1970) note which bivalve species are associated with particular

TABLE 1. Freshwater bivalves of Washington. Derived from Burch (1972, 1973) and Henderson (1929).* Species are listed in Henderson (1929).

Mollusca
Pelecypoda
Unionacea
Margaritiferidae
Margaritifera falcata*
Amblemidae
Gonidea angulata*
Unionidae
Anodonta kennerlyi*
A. oregonensis*
A. californiensis*
Sphaeriacea
Sphaeriidae
Sphaerium nitidum
S. patella*
S. lacustre
S. partumeium
S. securis
Pisidium idahoense*
P. casertanum
P. compressum*
P. ferrugineum
P. liljeborgi
P. nitidum
P. rotundatum
P. variabile*
P. ventricosum
P. conventus
P. insigne

cultural phases on the Lower Snake River (Table 3). Although subsequent research (Bense, 1972; Brauner, 1976; Kennedy, 1976; Rice, 1972; Yent, 1976) has altered the original cultural chronology slightly (Leonhardy, 1975) to that shown in Table 3, studies of faunal remains (Gustafson, 1972; Lyman, 1976) have done little to alter the

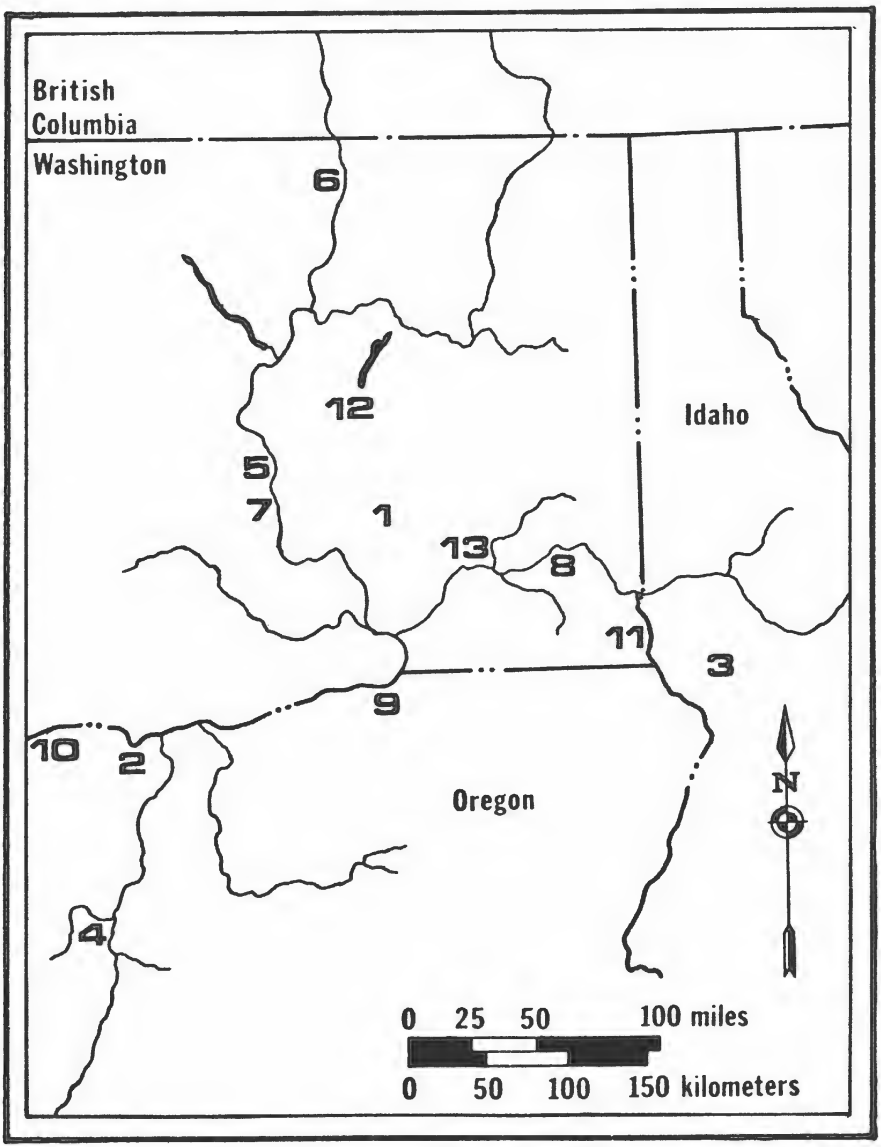

Figure 1. Archaeological sites and geographic locations mentioned in text. 1. Lind Coulee (45GR97). 2. The Dalles (35WS4). 3. Camas Prairie. 4. Round Butte. 5. Sunset Creek (45KT28). 6. Okanogan Valley. 7. Vantage. 8. Lower Snake River Region. 9. Cold Springs (35UM5). 10. Hamilton Island. 11. Scorpion Knoll (45AS41). 12. Grand Coulee. 13. Marmes Rockshelter (45FR50).

faunal sequence, particularly the bivalve chronology. Leonhardy and Rice (1970: 14) do note that "for the only time in regional prehistory, river mussels (*M. falcata*) seem to be an economically important resource rather than an occasional dietary adjunct" during the Tucannon Phase. Materials from the Cold Springs Site (35UM7) also suggest a heavy reliance on mussels near the end of the site's major occupation which typologically fits the Late Cascade and Tucannon phases of Leonhardy and Rice (Shiner, 1961: 187-191, Plates 34a and 35b). Regarding this apparent increased reliance on river mussels, Kennedy (1976: 64) has suggested "it can not be stated conclusively that utilization of freshwater molluscs is a characteristic of the Tucannon Phase." Quantitative analyses of molluscan remains may serve to resolve these differing interpretations.

Brauner's (1975) analysis of the Scorpion Knoll Site (45AS41) materials resulted in the delimitation of an early component (5000 to 2500 B.P.) and a late component (after 2500 B.P.). Brauner (1975: 23) states "the topographic position and cultural content of the Scorpion Knoll Site suggests a strong emphasis on gathering riverine resources with a marked de-emphasis on big game hunting and gathering plant resources." A primary activity was mussel collection as suggested by the high frequency of *M. falcata* shells, particularly during the early component (Brauner, 1975: 24). Reviewing geological data and inferred climates, Brauner (1975: 28) suggests that an increase in effective precipitation between 400 and 3500 B.P. resulted in the washing of volcanic ash originating from Mt. Mazama in 6700 B.P. into the river. These "suspended ash particles mechanically destroyed the fishes' gills. As a result, fish populations may have been decimated beyond the point of practical exploitation." Thus,

TABLE 2. Bivalve sequence from the Vantage area. Derived from Swanson (1962:31).

Years B.P.	Cultural Phase	Cedar Cave	Shalkop Site
	Cayuse 3		
		Margaritifera falcata	
	Cayuse 2	**Gonidea angulata**	
	Cayuse 1		
1750			
			M. falcata
	Frenchman Springs 3	**M. falcata**	**G. angulata**
	Frenchman Springs 2		
3000			
	Frenchman Springs 1	**M. falcata**	**M. falcata**
4250			
	Vantage 2		
7000			
8500	Vantage 1		

TABLE 3. Bivalve sequence in the Lower Snake River Region. Derived from Leonhardy and Rice (1970), and Landye (1973).

Years B.P.	Cultural Phase	Bivalve Sequence
180	Numipu	**Margaritifera falcata**
	Late Harder	**M. falcata** (high incidence)
2500	Harder	**Gonidea angulata** (low incidence)
4500	Tucannon	**M. falcata** (low incidence)
	Late Cascade	**G. angulata** (high incidence)
		Mazama Ash
		6700 B.P.
8000	Early Cascade	**M. falcata** (low incidence)
	Windust	**G. angulata** (high incidence)
10,000		

while the first component was being deposited (during the more effective precipitation period), mussels became an important dietary adjunct, replacing in part the decimated salmon resource. Amelioration of the climate beginning with the late component lead to an increased salmon population, and a reorientation of subsistence activities to emphasis on salmon and a decreased emphasis on mussels (Brauner, 1975).

One major factor makes Brauner's hypothesis unacceptable. "Freshwater mussels always attest to the presence of fish in streams from which they are collected since these mussels are obligatory parasites on fish during their young, or glochidial, stages" (Roscoe, 1967: 13). A decrease in fish population would result in a concomitant decrease in the mussel population. It could be argued that "several kinds of fish must be capable of serving as hosts" (Roscoe, 1967: 14), but I doubt mechanical destruction of fish gills by volcanic ash would have been restricted to salmon.

If the fish population was indeed decimated, the mussel population would have been under extreme stress to maintain its population size. Addition of a second stress factor—intensified exploitation by man—would have quickly decimated the mussel population. This occurrence might be reflected archaeologically by a decreased mussel size as intensified exploitation would affect a more rapid turnover of age classes with the consequence of a general reduction in age range and hence overall individual size in mussel population. An alternative or additional archaeological implication might be larger than normal size juveniles (i.e., displaying juvenile traits) due to the reduced intraspecific competition for food and a resultant potential increase in growth rate (see Swadling [1976] for a more detailed discussion of these phenomena). Response time of the mussel population to two adverse factors (environmental-reproductive stress and intensified exploitation) would probably be very rapid, and in a few tens of years the mussels would be too small in size and/or number to warrant exploitation.

Thus it seems we must reject Brauner's (1975) hypothesis and a similar one posited by Shiner (1961). Determination of whether an intensified exploitation of bivalves actually occurred and the causal factors for such intensification may be delineateable by studying age and size structure of archaeological mussel populations.

Perhaps the single most significant study of Southern Plateau mollusc remains is Landye's (1973) discussion of *Margaritifera* and *Gonidea* shells recovered from Marmes Rockshelter (45FR30) sediments (see Table 3).

> Changes in protein sources can be demonstrated by the pelecypod remains found in Marmes Rockshelter. Cultural units below the Mazama volcanic ash layer (6700 B.P.) have a high incidence of *Gonidea angulata,* but post-Mazama units produced a higher number of *Margaritifera falcata.* This may have been due to changes in Early Man's food preferences, local availability of clams, or populations of another protein resource, fish. Population numbers of *Salmo* sp., which serve as an intermediate host for the glochidia of *M. falcata* or the unknown fish host of the young *G. angulata,* may have fluctuated due to environmental stress. Whichever occurred, the result was a change in diet for Early Man at Marmes Rockshelter (Landye, 973:34-35).

Assuming representative samples were used, the change in taxonomic abundance recognized at Marmes Rockshelter may have very important ramifications in Southern Plateau prehistory. This observation becomes especially true in light of Swanson's (1962) recognition of a later shift from only *M. falcata* to *M. falcata* and *G. angulata* (see Table 2). I have combined the Marmes and Vantage bivalve sequences into the single, tentative Columbia Basin Bivalve Sequence presented in Table 4. The questionable assumption in-

volved is that causal factors were Columbia Basin-wide, and the molluscan and/or human response was similar throughout the area.

Pelecypod Ecology

In apparent descending order of abundance, *Margaritifera*, *Gonidea*, and *Anodonta* were exploited as a food resource during the prehistory of the Southern Plateau. To understand fully the significance of finding the shells of these taxa in archaeological contexts, one must have some knowledge of their ecology. This information is presented in Table 5.

In a general way *Margaritifera* ecology differs from *Anodonta* and *Gonidea*, which have similar requirements. This difference may suggest a reason for the dominance of *Margaritifera* in archaeological samples as human preference in mussels or habitats exploited. However, *Margaritifera* normally outnumber *Gonidea* 9 to 1 "in the region today, according to Joseph P. E. Morrison of the National Museum" (Swanson, 1962: 24). If this statement is true, then perhaps the archaeological relative abundances are simply a reflection of natural abundances, and no selection for one taxon of mussel was practiced by prehistoric peoples.

Assuming that no human selection was involved, the shifts in relative abundance suggested in Table 4 might be explained as responses of the bivalve population to marked

TABLE 4. Columbia Basin bivalve sequence. Derived from Tables 2 and 3.

Years B.P.	Bivalves
1000	**Margaritifera falcata**
	Gonidea angulata
2000	**M. falcata**
	G. angulata
3000	
4000	**M. falcata**
5000	**M. falcata**
6000	**M. falcata** (high incidence)
	G. angulata (low incidence)
	Mazama Ash
	6700 B.P.
7000	**M. falcata** (low incidence)
	G. angulata (high incidence)
8000	
	M. falcata (low incidence)
9000	**G. angulata** (high incidence)
10,000	

TABLE 5. Southern Plateau Unionacean bivalve ecology.

	Water Conditions	Substrate Type	Host
Margaritifera	prefers rivers, may be in lakes; fairly rapid current; prefers 1 m depth, occurs in ½ to 1½ m depth	prefers sand and gravel, sand behind boulders; generally absent from muddy areas	prefers trout (**Salmo** sp.), may use minnows (Cyprinidae) (attaches to gills)
	Comments: doesn't bury itself as deep as **Anodonta**; supposedly better eating than **Anodonta**		
Anodonta	found in reservoirs, rivers streams	prefers muddy bottoms, does occur elsewhere	prefers minnow **Gila** sp., may use other taxa (attaches to fins)
Gonidea	found in creeks, rivers, and lakes; may prefer rapid current; occurs in ¼ to ½ m depth	prefers muddy bottoms	

changes in stream regimes which in turn suggest climatic changes. This postulation seems unlikely, however, because of the relatively mutually exclusive habitats occupied by the bivalves. If one considers the microenvironmental conditions of the Columbia and Snake river drainages, it seems feasible that all three taxa could occur in their own specific habitat yet still be found in one linear kilometer of river in certain areas! Changes in stream or river regimes may destroy several habitat localities for a taxon but very probably will concurrently open up or create several new habitat localities a short distance away. Because the bivalves can occur outside of their preferred habitat (Ingram, 1948; Roscoe, 1967), colonization of new habitat areas need not originate from the destroyed habitat area.

The opposing argument, that human selection *is* reflected by the relative abundances of different taxa, seems unlikely as well. River mussels were apparently never more than a dietary adjunct for prehistoric peoples. It seems unlikely that human selection would play a major role in exploitation of a minor food resource.

The most pragmatic explanation would seem to be prehistoric Southern Plateau peoples exploited what was locally available. Schroedl (1973) has suggested that bison (*Bison bison*), while intermittently available to Columbia Basin occupants through the last 10,000 years, were apparently not specially treated or hunted with special weapons; instead, they were exploited if and when available at least during the last 3000 years. Ethnographic data indicate that subsistence practices as a whole were oriented towards exploiting what was available when and where it was available (Ray, 1933; Spier, 1938). All things considered, it appears that people probably exploited the taxa of bivalves that were available near the site. This hypothesis could easily be tested by selecting sites adjacent to different mussel habitats and identifying the shell from each site. For example, a site with mud-bottom sloughs nearby would be expected to produce mainly *Gonidea* and *Anodonta* shells; alternatively, riverine sites next to riffles or rapids with sandy, gravelly bottoms should contain shells of *Margaritifera*, assuming no change in immediate river habitats through time. Changes in molluscan faunas through time would suggest *local* variations in river mussel habitats and *perhaps* different stream regimes and environments.

A Description of Margaritifera, Gonidea, and Anodonta

The discussion above indicates much remains to be learned regarding bivalve ecology and prehistory. In order to facilitate study, field and laboratory identification of shells must be rapid and accurate, and the following descriptions are meant to be used in such endeavors. One should also refer to papers by Burch (1972, 1973), Henderson (1929), and Ingram (1948) which contain other illustrations. I must note that these descriptions are no substitute for comparative specimens. However, the collections I am familiar with are very deficient in freshwater bivalve specimens from the geographic area under discussion, and these descriptions may suffice until such time as more adequate collections are available. Only the three bivalve taxa used as a prehistoric food source (*Margaritifera*, *Gonidea*, and *Anodonta*) will be described.

The sketches presented as Figures 2, 3, and 4 illustrate the basic morphological differences of the shells and supplement the following descriptions:

Margaritifera falcata—two highly developed pseudocardinal teeth on large specimens of

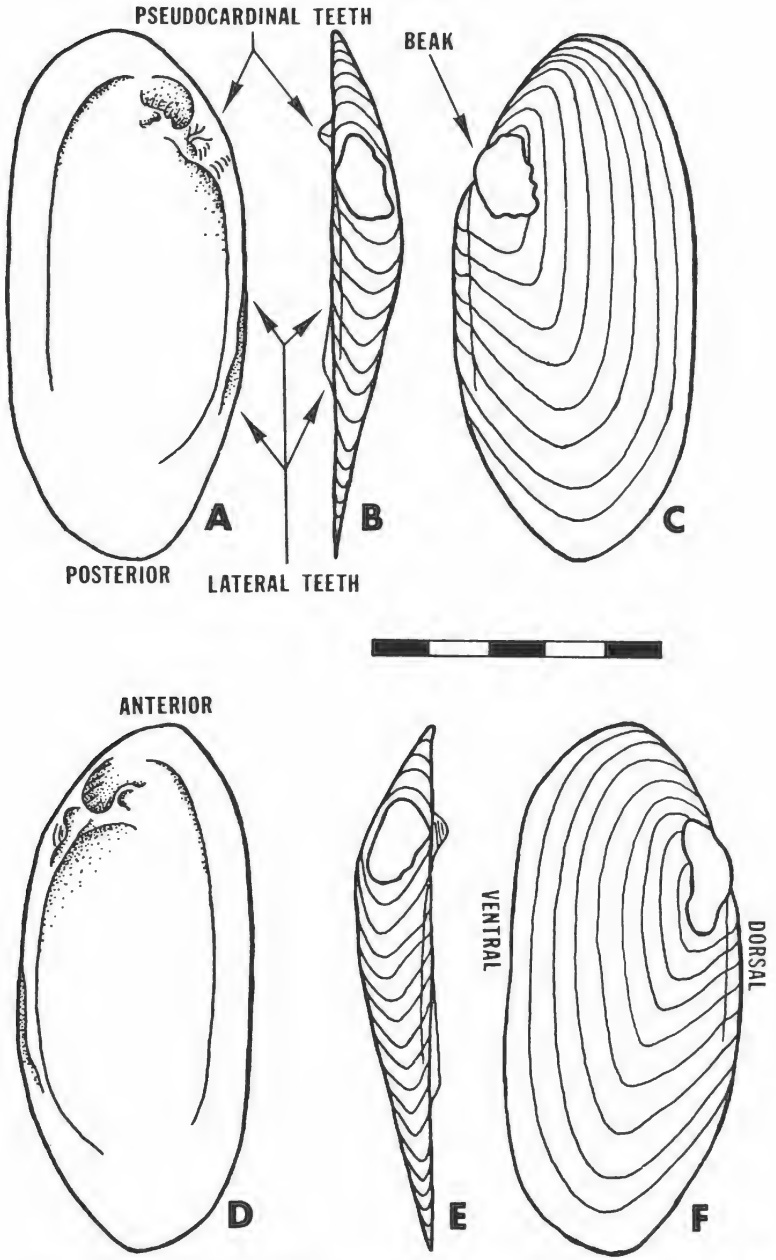

Figure 2. *Margaritifera falcata.* Land marks mentioned in text are labeled. Scale is 5 cm. A. Right valve, interior aspect. B. Right valve, dorsal view. C. Right valve, exterior aspect. D. Left valve, interior aspect. E. Left valve, dorsal view. F. Left valve, exterior aspect.

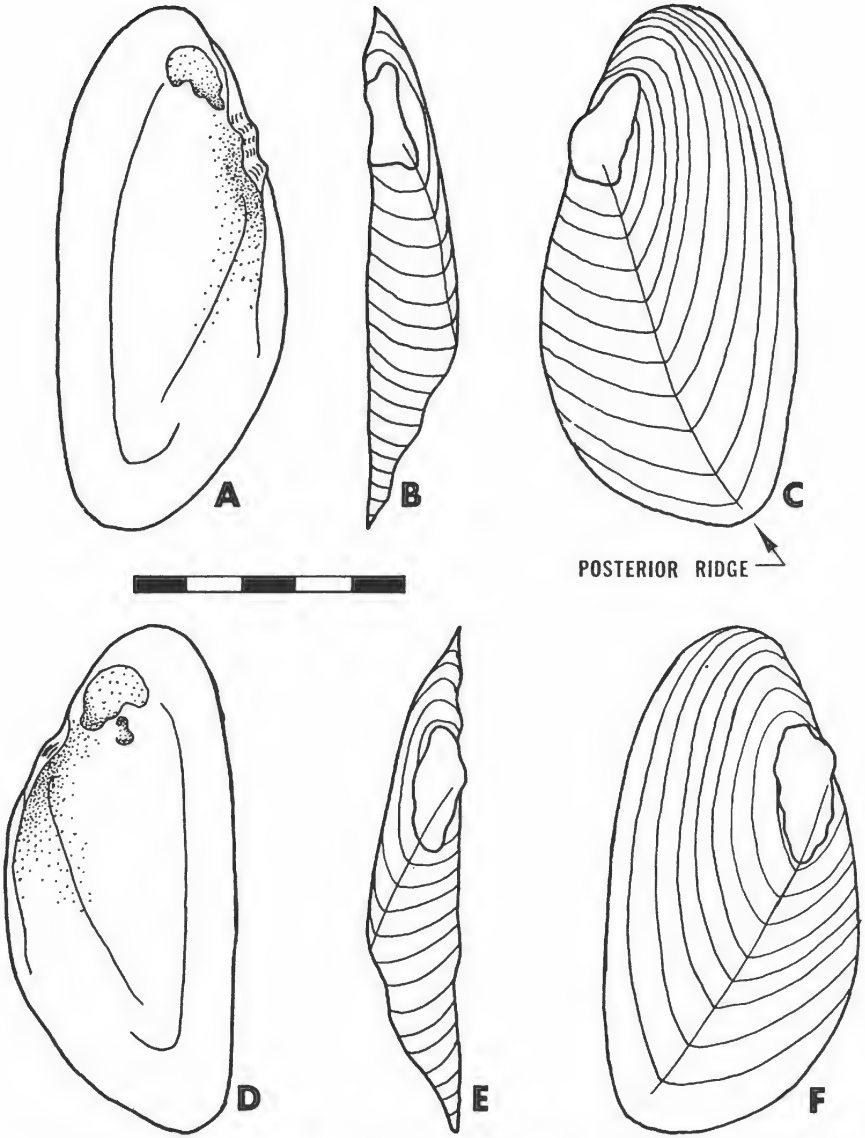

Figure 3. *Gonidea angulata.* Land marks mentioned in text are labeled. Scale is 5 cm. A. Right valve, interior aspect. B. Right valve, dorsal view. C. Right valve, exterior aspect. D. Left valve, interior aspect. E. Left valve, dorsal view. F. Left valve, exterior aspect.

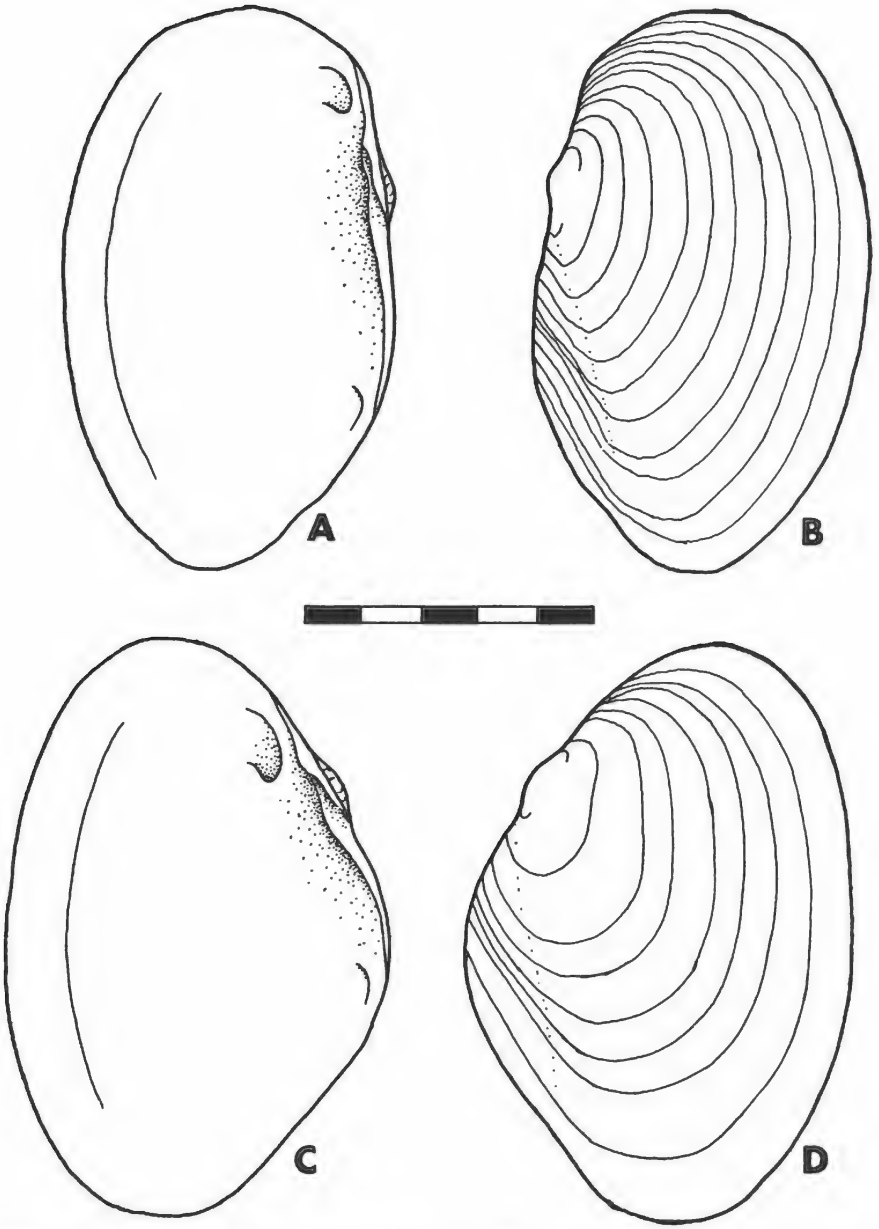

Figure 4. *Anodonta* spp. Scale is 5 cm. A. *A. oregonensis*, right valve, interior aspect. B. *A. oregonensis*, right valve exterior aspect. C. *A. californiensis*, right valve, interior aspect. D. *A. californiensis*, right valve, exterior aspect.

right valve, usually only posterior pseudocardinal tooth well developed on left valve; well developed lateral teeth or lamellae on both valves; shell generally elliptical in outline; beak usually concentric and pronounced; pronounced concave interior shell under lateral teeth.

Gonidea angulata—pseudocardinal teeth poorly developed if present, often only shallow troughs and low ridges; lateral teeth not as distinct as in *M. falcata*; pronounced posterior ridge; slight concave interior shell under lateral teeth.

Anodonta oregonensis—no pseudocardinal teeth; lateral teeth present and well developed but indistinct and small; shell elliptical in outline; beak concentric but not as pronounced as in *M. falcata*; slight concave interior shell under lateral teeth.

Examples of comparative specimens of *M. falcata* and *G. angulata* are presented in Figures 5, 6, 7, 8, 9, and 10. Archaeological examples of *M. falcata*, the most common mussel in archaeological deposits, are shown in Figure 11.

Summary

A review of mollusc analyses reveals several potentially fruitful lines of research regarding the natural and cultural prehistory of the Southern Plateau culture area. It is hoped the discussion will serve as an impetus for and aid in future research using the often disregarded river mussel.

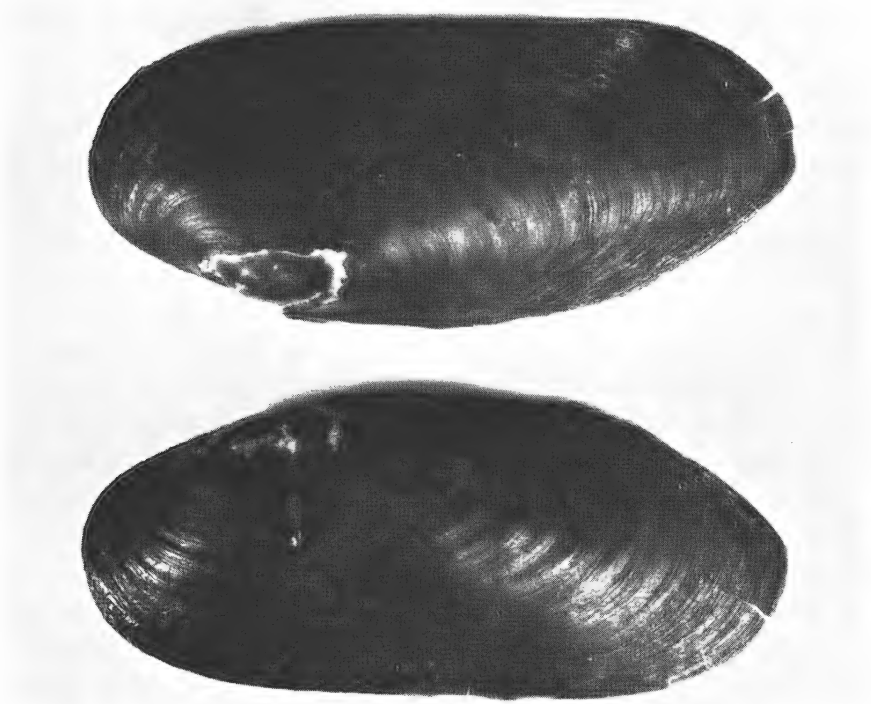

Figure 5. *Margaritifera falcata*, exterior aspect.

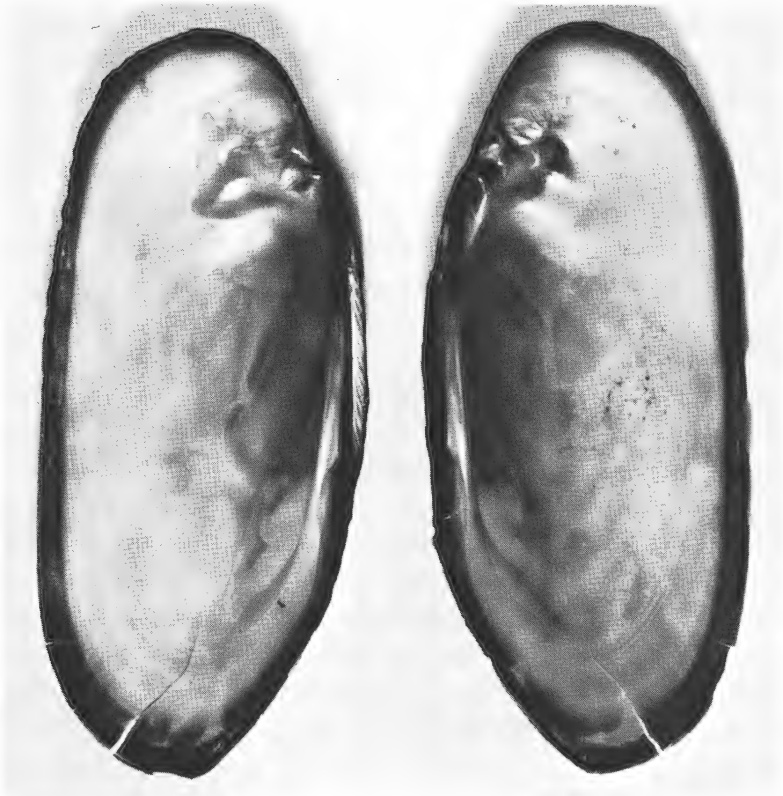

Figure 6. *Margaritifera falcata,* interior aspect.

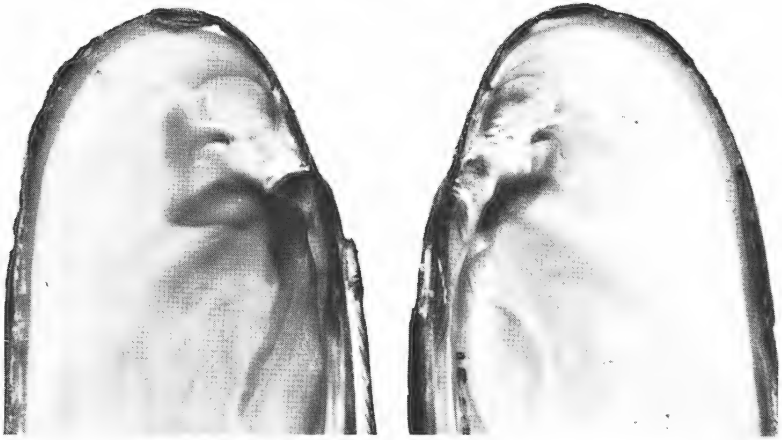

Figure 7. *Margaritifera falcata,* detail of interior aspect showing pseudocardinal teeth.

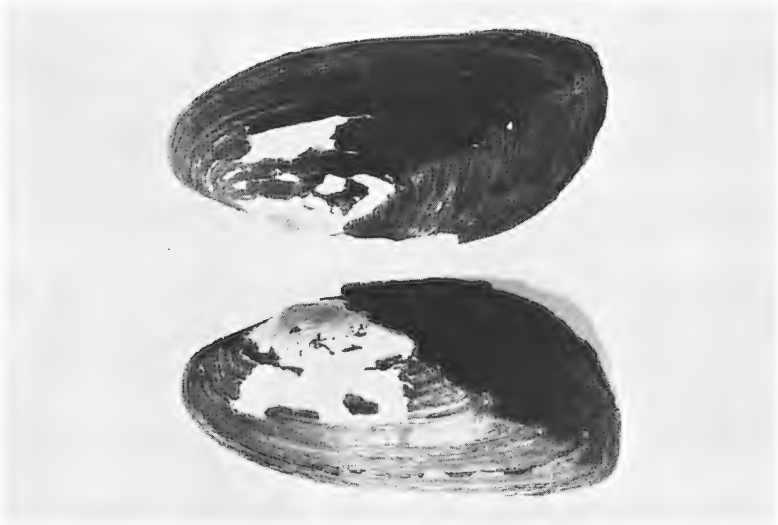

Figure 8. *Gonidea angulata*, exterior aspect.

Figure 9. *Gonidea angulata*, interior aspect.

Figure 10. *Gonidea angulata*, detail of interior aspect showing lack of pseudocardinal teeth.

Figure 11. Archaeological examples of *Margaritifera falcata* from north-central Washington.

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Characteristics of *Armillaria mellea* on Pine Root Systems in Expanding Centers of Root Rot

Abstract

Characteristics of infection and decay on ponderosa pine roots within, at, and beyond visible margins of actively expanding centers of Armillaria root rot were investigated through extraction of 320 root systems and *in situ* excavations across the perimeters of eight infection centers. Infection on lateral roots was common, and consistently resulted in formation of resinous lesions at attack points that frequently girdled and killed the roots. Colonization by *A. mellea* was commonly found distal but rarely proximal to lesions on living roots. Lethal attacks on saplings and pole-sized trees were regularly located high on the tap root or at the root collar. Over 40 percent of the trees along the most actively expanding margin of five centers were killed within two years. After tree death, the fungus rapidly colonized the major part of the root system. A linear equation was developed to estimate the distance beyond the outermost dead tree of active disease centers that infected root material extended. These estimates provided a basis for control action to halt further infection center enlargement through disruption of the root network responsible for continued pine to pine disease spread. A hypothesis on the dynamics of infection center development is presented.

Introduction

Productivity on several hundred hectares of ponderosa pine (*Pinus ponderosa* Laws.) forest land in south-central Washington has been greatly reduced through enlarging centers of root rot caused by *Armillaria mellea* (Vahl. ex Fr.) Quél. (Shaw *et al.*, 1976; Roth *et al.*, 1977). As seen aboveground, centers consist of a few live seedlings or saplings near old-growth pine stumps of trees cut 5-35 years earlier. Radial transects extending outward from tree-free parks that surround these stumps cross concentric rings of silvered windfalls of increasing diameter, stubs, black snags, and finally dying or recently killed trees.

While diagnostic for Armillaria root rot, these symptoms reflect the little studied underground development of the disease. Details of underground development of *A. mellea* among coarse roots of sapling and pole-sized *P. ponderosa* were investigated here through stump extraction and *in situ* root system excavation (Shaw and Roth, 1974).

Methods

Root systems of 320 living, moribund, and dead pines, situated in or near four discrete infection centers of Armillaria root rot, were unearthed by machine. The light pumice soil allowed extraction with minimum damage to roots. Soil remaining on roots was removed with hand tools. Observations were made on characteristics of *A. mellea* on each root system.

Segments 10 to 16 cm in length having mycelial fans in the cambial region were cut

from lateral roots and incubated at room temperature in plastic bags of moist quartz sand. Resinous root lesions representing points of attack by *A. mellea* (Adams, 1972) were similarly treated. These samples were examined periodically during two years for production of rhizomorphs. This method provided a measure of fungal viability (Redfern, 1968).

Exposure of roots *in situ* was accomplished by excavating trenches at right angles across the perimeters of eight actively enlarging infection centers. Trenches 12 to 16 m long extended from where stubs and snags were abundant outward into the healthy stand. One side of each trench was carefully excavated with hand tools for a distance of 1.2 to 1.8 m back from the face and 0.6 m deep. This depth unearthed over 80 percent of the roots (Shaw, 1975). Infected root segments collected along seven transects were incubated in moist sand as described above.

In addition to root examinations, observations were made on the rate of enlargement of infection centers as reflected by tree mortality. One hundred eighty-three healthy-appearing trees growing within 4 m of the nearest Armillaria-killed tree were marked around five infection centers. After two years, root rot mortality among marked trees was recorded.

Results and Discussion

Infection of Individual Trees

Characteristics of *A. mellea* on roots of extracted trees were similar to observations by Adams (1972). Infection on lateral roots was common and consistently resulted in resinous lesions at the point of attack. Over 600 root lesions were examined. Lesions ranged from 0 to 38 per tree (many trees had 10 to 20 separate lesions) and were easily recognized as concretious lumps of soil, rock, and resin around the infection site (Fig. 1). Rhizomorphs were often embedded in the matrix. Flow of resin frequently girdled the root leading to death, colonization, and decay by *A. mellea* of the distal portion. Occasionally, lesions were only small, resinous patches along an otherwise healthy root.

Only rarely, and then to a limited extent short of the root collar, had the fungus advanced proximally along a living lateral root from a girdling lesion. Observations on other conifers would suggest that attacks on live roots of vigorous trees behave similarly (Buckland, 1953; Patton and Riker, 1959; Rishbeth, 1972). This characteristic differs from the development of *A. mellea* on roots of hardwood hosts where the fungus does grow internally within a lateral root to the root collar (Zellar, 1926; Peace, 1962).

From aboveground symptoms, 50 of the 320 extracted trees (16 percent) were killed by root rot; 44 (88 percent) had a distinctive point of attack, a lesion with heavy resin production, and rhizomorphs and/or mycelium at the root collar or high on the tap root. These symptoms and signs are characteristic of young *P. ponderosa* killed by root rot. Three remaining root systems were too damaged for accurate observation and actual points of attack were unclear on the other three.

The regularity of attacks high on the tap root or root collar of killed pines, the rarity of fungal advance proximally from a lesion on a live lateral root, and the existence of living, apparently healthy trees with numerous lesions on lateral roots, but no tap or collar infection, supports Adams' (1972) suggestion that this location on the root system is the critical region for lethal Armillaria attacks on young ponderosa pine. As most of the Armillaria-killed pines examined had many lesions on lateral roots in addition

Figure 1. Pitch-encrusted lesions resulting from infection by *A. mellea* on a lateral root of *P. ponderosa.* Rhizomorphs were frequently found on the outside and within the resin-soil matrix of such lesions. On living roots the fungus commonly colonized root tissue distal to such lesions, but rarely advanced proximally within the root.

to the lethal attack, no fungal specialization to the tap root is indicated. The tap root presents a large target for rhizomorphs, and, as described later, it is eventually attacked through progressive expansion of infection centers. This behavior is consistent with descriptions by Patton and Riker (1959), Sokolov (1964), and Hintikka (1974) for other coniferous host species.

Extent of root system deterioration (wood decay as opposed to infection) corresponded with the aboveground appearance and location of killed trees. *A. mellea* was present and viable throughout root systems of dead trees, even in pencil-sized and smaller roots. *A. mellea* was decaying internal sapwood. Detailed root weights and fungal isolations across a root rot center from origin to beyond the visual limits support these observations (Shaw, 1975).

Typical Armillaria infection centers in sapling and pole-sized *P. ponderosa* have a

distinct, concentric zone containing stubs of trees dead for 15 or more years that have broken off near ground level (Roth *et al.*, 1977). Root systems of these stubs no longer have intact lateral roots and resemble carrots. These "carrots" still contained viable *A. mellea* as evidenced by fresh rhizomorphs, mycelial fans, and cultures obtained from decayed root wood.

Vitality of Infected Tissues

Thirty-three of 156 (22 percent) of the root lesions and infected root segments collected from extracted trees and incubated in moist sand produced rhizomorphs. In the trenches nearly all samples from infected roots immediately around or from the outermost dead tree produced rhizomorphs. In five transects, infected root material from the region where infected, and healthy roots intermingled produced rhizomorphs in sand culture. This is the region where new attacks are present on roots of otherwise healthy trees (Figs. 2, 3).

Infection at the Stand Interface

All eight transects showed sharp transitions between underground zones of infected and healthy roots and visible aboveground limits of infection centers. Inward from these visual limits nearly all roots, regardless of size or source, were infected with *A. mellea* (Figs. 2, 3). Beyond the visual limit, infected material consisted predominantly of roots of the outermost dead tree and occasional new lesions on otherwise healthy roots of outwardly adjacent living trees (Figs. 2, 3).

As apparent on the extracted stumps, colonization by *A. mellea* occurred distal but rarely proximal to resinous lesions on living roots. New infections were most abundant on living trees adjacent to the outermost dead trees and occurred on the side of root systems away from the healthy stand. These infections occurred most often at points on living roots in contact with or near (i.e., within centimeters) infected roots extending from previously killed trees. Disease transmission where root contacts or grafts are absent is probably by rhizomorphs which were common along infected roots and at lesions. Inoculation of seedling *P. ponderosa* with isolates of *A. mellea* obtained from this study area showed that infection consistently occurred via a rhizomorph arising from the inoculum segment, attaching to and penetrating the host (Shaw, 1977).

As trees die successively, the infected root systems of the outermost dead trees serve concurrently as an inoculum source and as an avenue of fungal spread into yet uninfected pines. Thus, infection centers continue to enlarge through repeated spread from pine to pine (Figs. 2, 3).

Tree Mortality at the Stand Interface

Between 1971 and 1973, 43 percent of the trees marked along the margins of five infection centers died from root rot (Table 1). Trees from 5-to 46-cm d.b.h. were killed. These figures are likely to be the maximum mortality rate along the interface because live trees were initially selected and marked outward from the most actively expanding portion of the infection center perimeter.

Infection Outward from the Stand Interface

Distribution of infected root material beyond the visual limit of an infection center was related to tree size, as would be expected from variations in root spread among trees of

Figure 2. Root systems of sapling *P. ponderosa* excavated perpendicular to the perimeter of an Armillaria infection center. Tree 1 is the outermost dead tree of the center. All root material in the foreground of tree 1 and white (painted) roots beyond are infected with *A. mellea.* Tree 2 has been dead longer than tree 1 and the root system shows more extensive wood decay by *A. mellea.* Stakes mark 0.91 meter (3 ft) intervals.

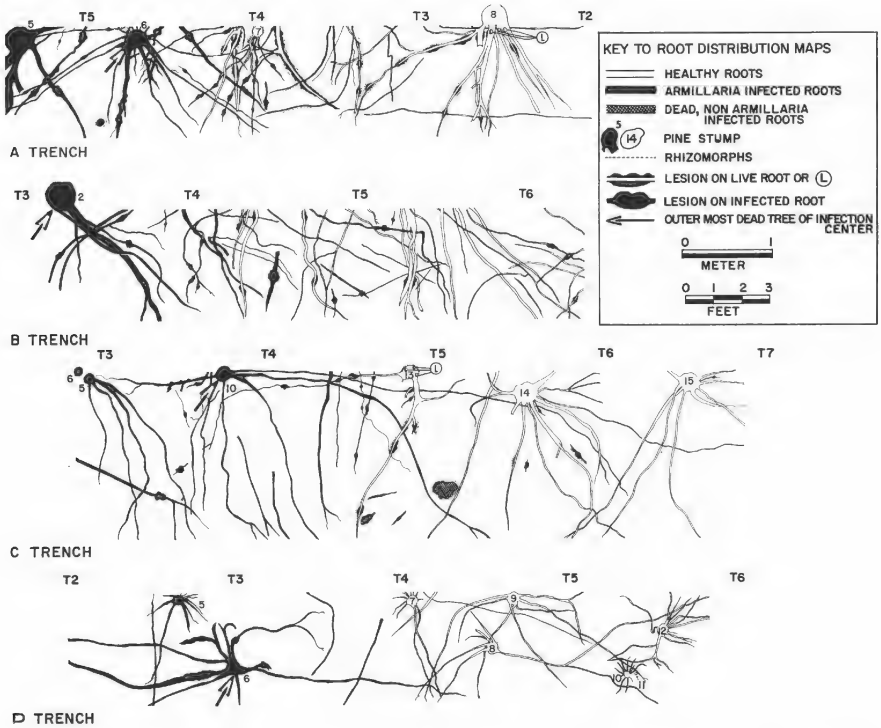

Figure 3. Root distribution maps from four of the eight transects excavated across the perimeter of actively enlarging centers of Armillaria root rot. Arrows point to the outermost dead tree of each center; healthy-appearing stand is to the right. Lesion on tree 15 (trench B) was not caused by *A. mellea.*

TABLE 1. Mortality after two years of healthy-appearing trees located at the outer visual limits of Armillaria infection centers.

Infection center	Number of marked living trees adjacent to the visual limit	Trees killed by **A. mellea** 2 years after marking	
		Number	Percent
1	36	18	50
2	32	15	47
3	39	13	33
4	39	17	44
5	37	16	43
Total	183	79	43

differing size. In the three transects with trees ranging from 8- to 15-cm d.b.h., infected roots of killed trees and lesions on living trees were not found beyond 3.2 m from the outermost dead tree. In centers with larger trees, up to 40-cm d.b.h., infected material extended as far as 5.5 m outward from the visual limit; more infected root material generally was present at all distances beyond the last dead tree than in centers among smaller stems.

Distance from the outermost dead tree to the limit of infected roots and new lesions was significantly related to mean d.b.h. for trees in which the center occurred ($F = 29.4$, 1 & 6 df; $P < 0.01$; $R = 0.91$). A linear regression equation developed from the eight excavations was used to estimate the distance from the bole of the outermost dead tree of a discrete infection center to the limits of infected root material and points of new attack in trees of various size (Table 2).

All trees killed by *A. mellea* in the five infection centers monitored (Table 1), including the few that died beyond the marked stems, were within the confidence limits of exposure distances predicted by the equation. Values in Table 2 are also accurate for commercial timber marking practices aimed at disease control through disruption of the root network responsible for continued disease spread (Fig. 3). These values are currently being used for root rot control where conditions are appropriate (Roth *et al.*, 1977; Roth and Rolph, 1978).

TABLE 2. Confidence intervals (95 percent and 99 percent probability levels) on the distance that infected root material extends beyond the visual limits of expanding infection centers of Armillaria root rot.[1]

Tree size	Confidence interval (distance)	
	95 percent probability level	99 percent probability level
	m	m
Saplings		
13-cm d.b.h or less	3.9-4.6	3.7-4.8
Small poles		
15-23-cm d.b.h.	4.4-5.4	4.2-5.6
Large poles		
25-41-cm d.b.h.	5.1-6.7	4.6-7.1

[1]Based on the linear equation, Y (distance in meters that infected root material extends beyond the bole of the outermost dead tree of the infection center) = 2.63 + 1.28 X (mean d.b.h. in cm of trees within which the center occurs), that was obtained by regression analysis of the distances and tree sizes in 8 excavations.

Infection Center Dynamics—A Hypothesis

In summary, the following sequence of host-fungus interactions appears operative in expansion of infection centers of Armillaria root rot in ponderosa pine in south-central Washington.

After timber harvest, *A. mellea*, growing as a perthophyte distal to quiescent lesions on roots of old-growth pines (Shaw, 1975; Roth *et al.*, 1978), colonizes the massive root systems of the stumps. Within five or six years (Shaw and Roth, 1976), this spread is indirectly evident in sapling mortality at the edge of the tree-free park that normally is formed under the old-growth crown.

Rhizomorphs from infected old-growth roots contact and penetrate roots of surrounding young growth that extend into the park area. The host responds with a flow of resin that occludes the fungus, confining it to a lesion at the infection site. Girdling lesions kill roots distally, allowing fungal colonization. The fungus generally does not advance proximally within the root as long as the tree remains alive. Interestingly, the resin which seems to occlude the fungus from proximal advance within the *in situ* live root can variously inhibit (Rishbeth, 1972) or stimulate (Shaw, 1975; Shaw and Roth, 1976) growth of *A. mellea* in culture.

While small trees may die quickly, larger trees may contain numerous lesions on lateral roots and remain alive. Eventually, rhizomorphs contact and penetrate the young tree high on the tap root or at the root collar. The host responds with the usual flow of resin. A root girdling, pitch-impregnated lesion results, stressing and eventually killing the tree. Death is likely hastened by the lack of summer moisture and high temperatures which cause further stress.

In dead trees the fungus continues to develop in the root collar area, forming distinctive mycelial felts under the bark. Downward from the root collar the fungus continues to grow through the cambium of the roots. It also advances proximally from lesions on lateral roots. In seedlings and smaller saplings, the tree apparently dries so that the tissue will no longer support growth of the fungus. In larger saplings and poles, root systems stay moist enough to allow the fungus to survive and initiate decay of root wood.

Rotting lateral roots of killed trees serve as avenues for spread of the fungus into adjacent heathy trees and the infection process is repeated, enlarging the center of continued spread from pine to pine. Estimates place the rate of expansion in the study area near 1.0 m/year (Shaw and Roth, 1976) where stocking density and other environmental features are favorable.

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Mountain Topography and Vegetation Patterns

Abstract

In the northern Rocky Mountains, topographic control over microclimates allows vegetation that is characteristic of subalpine environments to descend locally to very low altitudes, whereas steppe vegetation can be found locally at rather high elevations. Therefore, the significance of elevation above sea level has very little ecologic significance in this area.

Introduction

The progressive change in plant life observable wherever one ascends the mountains long ago stimulated attempts to divide montane vegetation into altitudinal zones, with quantitative altitudinal limits often suggested. So long as only a few very broadly conceived zones based on reconnaissance level observations were recognized, figures referring to their altitudinal limits were commonly accepted. But experience has shown that as the synecology of an area is carefully investigated, the concept of altitudinal zones weakens progressively. Some specific examples of this point, based on studies in northern Idaho and eastern Washington, are here presented.

Methods

The field work was based on analyzing landscapes from the standpoint of the type of potential (i.e., climax) vegetation that should develop in the absence of disturbance. Since most of the forest land has been logged, burned, or heavily grazed in the past century, the present developmental stages of the vegetation often bear little resemblance to the type to be expected when stability is attained. Such disturbance types usually have boundaries bearing limited relation to the physical environment, whereas climax types are closely coupled with a relatively fixed pattern of physical factors. Unless vegetation dynamics are emphasized, the order that exists in the field is obscured by the close resemblance that a disturbance type in one habitat type may bear to the climax type elsewhere.

Population structure is the key to understanding here. Seedlings or suppressed trees in the forest indicate the future dominants regardless of the character of the present overstory. Climax equilibrium can be recognized only when the compositions of the canopy and young trees are similar.

The Palouse Range

A striking illustration of the way topographic features may complicate the influence of altitude on vegetation may be observed on the Palouse Range in the western foothills of the Bitterroot Mountains. A few km north of Moscow, Idaho (Fig. 1), the south face of this Range rises abruptly from the basal plain to a crest more than 600 m above. This Range, as well as other mountains to the north and east, is forested, whereas steppe extends to the horizon on the south and west.

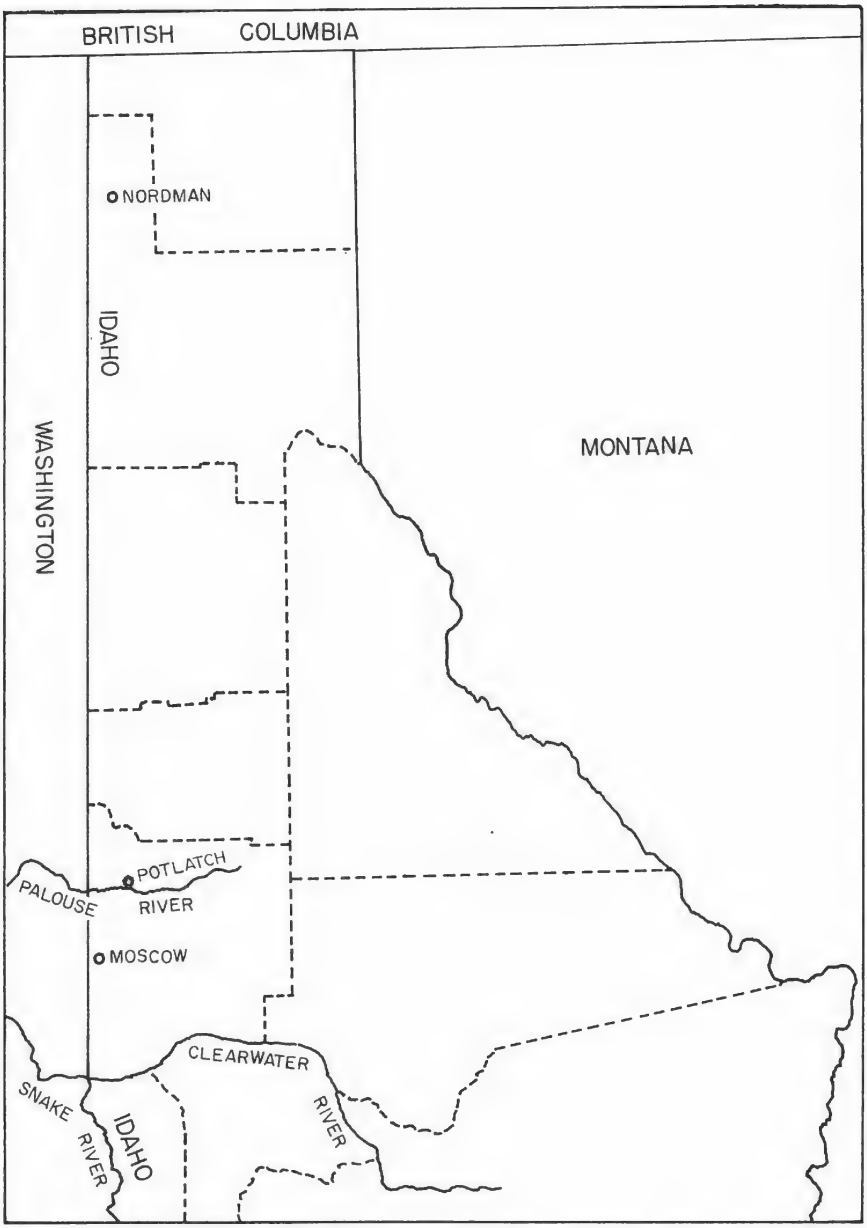

Figure 1. Northern Idaho showing the locations of cities and rivers mentioned.

By walking from the crest of the main ridge southward down the side ridges and valley bottoms to the edge of the basal plain, the altitudinal limits of the forest types have been obtained with an anaeriod altimeter. Such altitudinal determinations are only approximations owing to the necessity of depending on this instrument for many hours between opportunities to recalibrate it at a known benchmark.

Figure 2 is an elevational diagram in which no great attempt has been made to keep horizontal distance between topographic features proportionate, and only the principal valleys and contiguous ridges have been shown. The branching of the valleys is considerably more intricate than can be suggested on an elevational diagram, but this simplification does no violence to the basic pattern.

Two more or less independent zonal patterns are evident in Figure 1. By ignoring the valleys and confining attention to the interfluves that are fully exposed to sun and wind, one can recognize an east-west series of altitudinal belts which have a decided cant, with the ends toward the steppe lying at relatively high altitudes. Since these altitudinal belts rise as the mass of the ridge diminishes, the situation constitutes a local reversal of the Massenerhebung effect, in which the altitudes of macroclimates and biota normally increase as mountain mass increases. The explanation of the anomaly is obvious. On approaching the arid steppe, each forest belt finds suitable conditions at higher and higher altitudes, with lowered temperatures compensating as precipitation drops off.

A second evident system of zones is one that is repeated in the deep valleys that crease the face of the Range. Each deep valley contains a fusiform island of distinctive vegetation, oriented at right angles to the somewhat horizontal system of zones. Since these deep valleys open southward, sunlight penetrates to the bottom for only a short period of time centered on noon, so the valley-dependent system is relatively mesophytic. Starting very simply near the western extremity of the ridge, the vegetation of the fusiform islands becomes increasingly more complex to the east, until it consists of several concentric types, arranged in a series with the most mesophytic member deepest in the valley. An additional element of complexity, not shown, is that a line of *Picea engelmannii* follows the creek banks in each strip of *Thuja* forest.[1] The *Picea*, having seedlings that

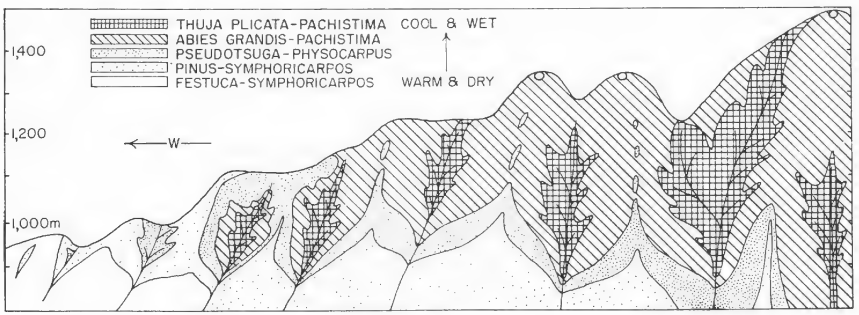

Figure 2. Elevational diagram showing the pattern of potential vegetation types on the south face of the Palouse Range, north of Moscow, Idaho.

[1]For descriptions of forest communities named, see Daubenmire and Daubenmire (1968).

require a more constantly moist soil surface, does not extend to either the upper or the lower extremity of the *Thuja* islands. For example, in the island opposite the highest point of the Range (i.e., Moscow Mountain), *Picea* occurs as a seral streamside species between the elevations of 900 and 945 m, whereas the *Thuja* island extends from 863 to 1158 m.

If one starts at the lower extremities of the deeper valleys and travels up the creeks, he encounters vegetation types in order from dry to moist, as is generally true whatever course one takes to leave the steppe and ascend the Bitterroots in eastern Washington and adjacent Idaho. But above the middle of the valley the order becomes reversed, and the higher he climbs the more xerophytic the vegetation becomes. The combined effects of increasing exposure to sun and wind coupled with the blow-over effect on precipitation, and good soil drainage, outweigh the drought-ameliorating influence of lowering air temperature.

Some temperature measurements in one of these valleys are significant. At the lowest end of the *Thuja* island, which is situated in the westernmost valley to contain such forest, daily maximum and minimum temperatures were measured at an elevation of 1 m above the soil surface. One station was in the *Thuja* strip along the creek, with another in the *Pinus ponderosa* forest on the ridge above, 90 m higher. During the month of study (22 June-20 July), there was a thermal inversion 93 percent of the nights, as well as 68 percent of the days. The ridgetop averaged warmer by 1.1°C during the day, and 8.2°C during the night.

Since studies of the soil moisture regime in this vegetation mosaic (McMinn, 1952; Daubenmire, 1968) have revealed a consistent trend of increasing dryness from *Thuja* to *Abies grandis* to *Pseudotsuga* to *Pinus* forest, it would appear that cold air drainage, often continuing during the day as well as the night, is an important factor maintaining the strong moisture gradient from valley bottoms to ridgetops.

In places where the crest of the main ridge has a slight dip with a projecting knob or lateral spur immediately west of this dip, the strips of relatively mesophytic vegetation extend up to and across the summit to become continuous with a more extensive body of the same forest type on the north slope of the Range. In these cases the south slope units are analogous to peninsulas rather than islands, although completely isolated fragments of all four major vegetation types occur elsewhere on the south slope of the Range. The farther from the west end of the Range, the greater the tendency for valley systems to be like peninsulas instead of islands.

Where the ridge crest is not marked by a protected dip, there is a very abrupt ecotone between a relatively xerophytic community on the south slope and a more mesophytic community on the north slope. The only exception is on the highest point (Moscow Mountain): Abies forest encircles the peak, although its expression on the south side is very impoverished.

A fourth noteworthy feature of the south slope is the nature of the vegetation just below the summits of each of the major prominences along the crest of the Range, especially West Twin, East Twin, and Moscow Mountain. Each of these places is occupied by vegetation which has wide distribution only at considerably lower altitudes. On West and East Twin the vegetation islands consist of a small savanna-like stand of a *Pinus-Pseudotsuga* intergrade. The pines that are in the open forests of these restricted areas suffer from wind breakage, but they are not noticeably dwarfed.

The xerophytic island at the top of Moscow Mountain consists of a spot of grassland which resembles very closely the *Festuca-Symphoricarpos* association on the adjacent basal plain, and is partly surrounded by an irregular zone of *Symphoricarpos* shrubbery. The slender fringe of *Pseudotsuga* which borders this park is open and savanna-like, with short trees having rapid taper. The environment here is so ill-suited to *Pinus ponderosa* that only one small specimen occurs at the upper margin of the park.

In no case does the vegetation of these exposed situations exhibit evidence of previous occupancy of the site by more mesophytic types. Nor is there any evidence that succession to a more mesophytic type is taking place at present. These island-like stands, as well as the special strips of valley vegetation, are therefore to be classed as topographic climaxes in equilibrium with a set of environmental factors inherent in their exposure or protection.

Every vegetation type from steppe to *Thuja* forest exists at elevations between 1000 and 1500 m on the south slope of the Palouse Range, and this vegetation mosaic is not an isolated extreme. For example, in the Clearwater Valley about 40 km to the south, similar topographic patterns in the vegetation can be found, and on a much larger scale.

Frost Pocket Effect

The vegetation pattern described above illustrates clearly how topographic control over the environmental water balance, improving it in some places and impairing it elsewhere, can over-ride the broad-scale influence of macroclimate in determining the plant-environment potential locally. Another type of environmental control, operating through temperature and apparently rather free of water balance, involves cold air drainage. Two examples follow.

The north-facing slopes of the Palouse River Valley approximately 15 km east of Potlatch, Idaho, support mainly an alternation of *Abies grandis/Pachistima* and *Thuja/Pachistima* habitats. The latter are restricted to valleys that crease the slope and extend up to an elevation of about 880 m, the former dominating the ridges between. This pattern extends down the valley sides to the river terrace forming the flat valley floor at about 780 m, where both habitat types end abruptly. The valley floor belongs to the *Abies lasiocarpa/Pachistima* habitat type, although clearing and grazing have left little more than *Abies lasiocarpa* and *Picea engelmannii* from the natural flora.

Owing to cold-air drainage, the valley floor is an elongated strip of land subject to frost any night in the year, and this frost apparently exceeds the tolerance of trees primarily adapted to oceanic climate, such as *Abies grandis* and *Thuja*, allowing continental species that are more frost-tolerant to retain dominance. The pennant-shaped islands of *Thuja*, which broaden downslope, abruptly and remarkably terminate at the very edge of the river terrace.

A much more common example of frost allowing trees characteristic of the highest forested ridges to descend to low altitude is the frost-pocket phenomenon. (The Palouse Valley is too long a strip to merit the term "pocket," although the vegetation phenomenon, if not the topography, is identical with that of the pocket.) A frost pocket is the result of a constriction in a valley where opposed spurs along the sides draw close together. Cold air draining into the valley flows down its gradient more rapidly than it can filter through the narrow gap between the spurs, so that each night a pool of cold air accumulates immediately above the bottle-neck.

A fine example of a frost pocket can be observed approximately 25 km east of Moscow, Idaho, where the highway to Deary drops briefly into the valley of Dry Creek. *Abies grandis/Pachistima* forest is the potential climax cover of north-facing slopes here, with *Pseudotsuga/Physocarpus malvaceus* in this role on south-facing slopes. Before the valley floor was nearly all cleared for agriculture, it was covered with *Abies lasiocarpa/Pachistima* forest. However, not even barley proved successful on this frosty surface, so unmanaged *Poa pratensis* pasture has become the principal land-use. The elevation of this frost pocket is approximately 820 m. Twenty-five km to the west, at Moscow, Idaho, *Festuca/Symphoricarpos* steppe covers the hilly topography to this elevation! Here again there is a sharp distinction between continental tree species on the valley floor, and the oceanic *Abies grandis* and *Larix occidentalis* (seral) on the valley sides. *Picea*, commonly a seral tree toward the wetter margin of the *Abies grandis* forest, here extends a short distance up minor ravines off the frost pocket.

Frost pockets closely similar to the above are common in the forests of northern Idaho and eastern Washington, and usually there is no evidence to indicate that the frost-tolerant *Abies lasiocarpa* and *Picea* are susceptible to eventual displacement by competitively superior trees. The sole exception thus far noted is as follows.

Where Granite Creek flows from Washington into Idaho at a point approximately 11 km northwest of Nordman, Idaho, opposed spurs of the valley sides come so close together that the creek once occupied nearly all the narrow gap. Even the construction of a one-lane road necessitated blasting away of the northern spur, and much more of the same was later needed to widen the road to two-lane status.

Immediately below the bottle-neck, *Tsuga heterophylla/Pachistima* forest occupies all slopes within sight of the road, extending to the very margins of Granite Creek. *Abies lasiocarpa* and *Picea engelmannii* are seral in this habitat type, and at present are of rare occurrence below the constriction.

Immediately above the bottle-neck, large trees of the *Abies* and *Picea* are abundant, with smaller trees of *Tsuga* and the seral *Thuja plicata* well represented among them. As one progresses along the road up the creek, *Abies* and *Picea* thin out, and beyond about 6.5 km from the constriction the *Tsuga/Pachistima* habitat type prevails even down to the creek margin. Since this point is approximately 60 m above the creek at the constriction, the pool of cold air that is ecologically critical may be (or was, prior to blasting) about 60 m deep at the constriction, if its surface is level. The environment in this frost pocket appears to have allowed *Abies* and *Picea* to gain dominance soon after the last devastating fire accentuated frostiness, with *Tsuga* and *Thuja* then benefiting from microclimate amelioration by the primary invaders to dominate reproduction later. Since *Thuja* is seral where it occurs on drained soils in this valley, *Tsuga/Pachistima* forest appears to be the potential climax in this frost pocket, as well as above and below it in the valley. The Granite Creek basin which collects the cold air exceeds 1000 ha in area, but the floor of the basin is tilted sufficiently that cold air accumulates in only a restricted area above the constriction.

Discussion

Interdigitation of vegetation types in the Rocky Mountains, with low-altitude types extending highest on south-facing slopes and ridges, whereas high-altitude types descend farthest along north-facing slopes and creek margins, has long been recognized (Dauben-

mire, 1943). The specific examples described briefly here emphasize the magnitude of overlap in their altitudinal ranges, and point out some local variations involving reversals of the general pattern. Clearly topographic influences on microclimate are so strong and pervasive in these forests that references to elevation above sea level have very low value for indicating the nature of the environment of an organism or a community. It is not difficult to characterize the absolute altitudinal limits of each specific community type, but their ranges overlap so greatly that their determination serves no useful purpose.

On the other hand, most of the montane communities in the Rocky Mountains can be aligned in an ecologically significant series reflecting an environmental gradient from warm-and-dry to cold-and-wet, irrespective of altitude. Although this series is often referred to as an altitudinal series, the expression must not be taken literally. It is this interdigitation of vegetation types which brings an ecologically wide variety of communities into close proximity, and it reduces the precision with which paleontologists can interpret the nature of past vegetation, especially from fossil pollens.

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Great Basin Pocket Mice (Perognathus parvus) in the Vicinity of Radioactive Waste Management Areas

Abstract

This study compares population parameters for Great Basin Pocket Mice residing near radioactive waste disposal sites and within a nearby protected (control) area. Mice emerged from below ground torpor in early spring (March), with males appearing earlier than females. Young-of-the-year first appeared in significant numbers during June. The ratio of males to females approximated 1:1, except during early spring months. Estimates of seasonal abundance showed peaks of 47 and 42 pocket mice per ha for disposal and control study areas, respectively. An estimate of pocket mouse biomass (g live weight) revealed peaks of 541 g/ha and 683 g/ha for disposal and control areas. The proportions of reproductively active males and females were equivalent on both study areas. Home range area estimates (m^2) are included.

Introduction

This study was designed to investigate the environmental health of a population of small mammals inhabiting an area adjacent to a radioactive waste disposal zone on the Department of Energy's (DOE) Hanford Reservation in Benton County, south-central Washington. The actual study location is designated as the B-C Cribs site and is centrally located on an elevated area known as the 200 Area Plateau, 750 ft above mean sea level.

Comparisons were made between populations residing near a waste disposal site and those occurring on the Arid Land Ecology Reserve (ALE) *ca.* 7 mi away at about the same elevation.

The plant community of both study sites is comprised of a sagebrush (*Artemisia tridentata*) overstory, with an understory dominated by cheatgrass (*Bromus tectorum*) and Sandberg bluegrass (*Poa sandbergii*). Other plant species such as rabbitbrush (*Chrysothamnus viscidiflorus* and *C. nauseosus*), needle-and-thread grass (*Stipa comata*), Indian ricegrass (*Oryzopsis hymenoides*), and thick-spiked wheatgrass (*Agropyron dasystachum*) are locally abundant.

The climate of the area is characterized by hot dry summers and cold winters with most of the precipitation occurring during fall and winter months. Precipitation averages about 20 cm per year.

Methods

Trapping grids were established in a 10 x 10 grid pattern at 10 m intervals. A Sherman live trap located at each station contained Dacron® batting and a small amount of mixed seeds thus providing nesting material and food. These precautions prevented captured animals from becoming torpid during confinement. Each trap was placed in a metal can and covered with a sheet-metal tent to shade it from direct sunlight.

During the first afternoon of the trapping session, the trap doors were opened and a small quantity of an oatmeal peanut butter mixture was placed on the door to serve as bait. Early the following morning, the traps were checked and captured animals examined. All animals were individually marked with a series of toe amputations for identification. The trap coordinate, species, sex, identification number, reproductive condition, relative age, pelage condition, and weights of all animals were recorded. After the captured animals were released, the traps were reset and checked in the same manner the next two mornings.

Reproductive condition was decided based on external signs. Males were classified as reproductively active when they had scrotal testes. Females demonstrated reproductive activity by changes in vulva shape and color during estrus, palpability of fetuses in the latter stages of pregnancy, and condition of the mammae during lactation. All females demonstrating signs of estrus, observable pregnancy, or lactation were considered reproductively active.

Age categories were limited to adult or subadult. Size-weight was the first criterion for assignment of an age category, as newly weaned subadults weigh about half of the average adult weight. The appearance of the pelage was also considered because the coloration and hair texture of subadults is usually different from that of adults.

Data gathered in the field were transcribed to a computer-compatible form for storage and retrieval. Monthly summaries, containing historical information for each individual, were generated at the close of every trapping session, providing a field diary for use during subsequent trapping sessions.

Results

The seasonal abundance of Great Basin pocket mice captures over 19 three-day sampling sessions is shown in Figure 1. The sessions occurred at monthly intervals and accounted for over 5000 trap nights. These values were derived from the number of individuals captured during monthly trapping sessions rather than from total captures, since recapture frequency varies through the year.

Pocket mice have a tendency to become trap prone after exposure to live-trapping. The extreme differences in the number of individuals captured during the initial two trapping sessions may reflect this effect (Figure 1) since the disposal plot had just been established, while the control plot had been trapped for several years as part of a separate study. During 1974, the pocket mouse population on the control plot remained higher than that found on the disposal plot. The 1975 data also exhibit a similar trend, although during June and July the number of individuals trapped on the B-C Cribs plot slightly exceeded the number trapped on the control plot. Heteromyid rodent populations have been shown to fluctuate in relation to the production of winter annuals (Beatley, 1969, 1976). The observed differences may result from differences in vegetation and seed production between the two study areas.

Estimates of population size were made using the Jolly-Seber (Jolly, 1965) stochastic model (Table 1). Estimates for inactive periods are not shown since they become unreasonable as a result of bias within the model (Gilbert, 1973). An estimate of pocket mouse density (no./unit area) was obtained from population size estimates, by considering the effective trapping radius of the study area. The trapping grid comprised 8100 m^2 (10 x 10 grid, spaced at 10 m intervals), O'Farrell *et al.* (1975) measured the

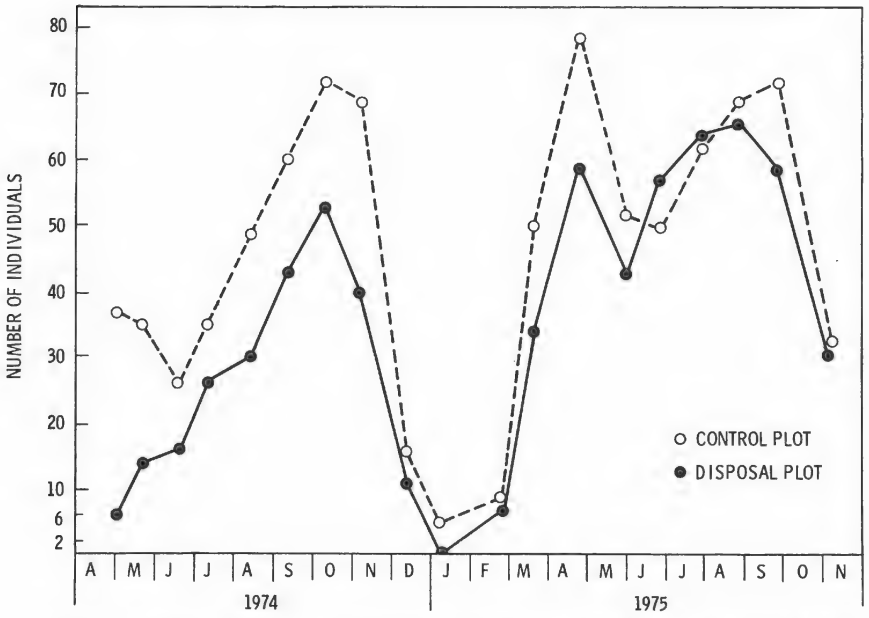

Figure 1. Seasonal abundance of pocket mice captured in Disposal and Control study areas.

effective trapping area for a population of pocket mice in a sagebrush/bunchgrass area on the ALE Reserve by establishing perimeter traps at successively greater distances from the central trapping grid. He found that a zone 25 m wide adjacent to the main grid served as an adequate buffer for estimating the effective trapping area. Since we found that the small mammal populations inhabiting the disposal and control study areas had similar sized home ranges as reported in O'Farrell's study, it seems reasonable to assume a similar sized buffer zone. The effective trapping area of the control grid and buffer zone would, therefore, equal 1.96 ha. This estimate was used in the denominator (no./unit area) to calculate pocket mouse density for disposal and control study sites shown in Table 1. Peak density occurred in March 1975 on the disposal plot with 47 individuals/ha as compared to a peak of 42/ha, which occurred in April 1975 on the control study plot.

Sex Ratio

A one to one sex ratio was expected for both study populations. An apparent unbalanced sex ratio occurred early in the 1975 season (Table 2). Males commenced aboveground activity earlier than females, creating a temporary imbalance in the sex ratio of the animals exposed to trapping rather than an imbalance in the population sex ratio. Peak adult numbers were observed in April 1975 on both plots. At this time, the sex ratios did not significantly differ from 1:1. The peak subadult populations observed on the disposal and control plots in 1974 occurred during October and November, respectively. In 1975 the subadult population peaked in August on the disposal plot and in September on the control plot. The proportion of reproductively active males and females followed

similar seasonal patterns during both study years. Analysis of proportions during peak adult population periods failed to detect significant differences between control and burial ground populations.

TABLE 1. Observed and estimated population sizes of **Perognathus parvus** computed using Jolly-Seber Stochastic model. (Jolly, 1965).

Date	Control Plot Numbers Observed	Control Plot Population Estimate	Control Plot Density[1]	Disposal Plot Numbers Observed	Disposal Plot Population Estimate	Disposal Plot Density[1]
3 May 74	37	35	18	6	13	7
23 May 74	35	35	18	14	13	7
21 June 74	26	38	19	16	15	8
12 Jul 74	35	42	21	26	26	13
15 Aug 74	49	54	28	30	39	20
13 Sep 74	60	70	36	43	48	24
10 Oct 74	72	80	41	53	57	29
7 Nov 74	69	*	*	40	*	*
12 Dec 74	16	*	*	11	*	*
9 Jan 75	5	*	*	0	*	*
27 Feb 75	9	27	14	7	55	28
20 Mar 75	50	50	26	34	92	47
24 Apr 75	79	83	42	59	67	34
30 May 75	52	56	29	43	44	22
26 Jun 75	50	53	27	57	59	30
1 Aug 75	62	62	32	64	66	34
28 Aug 75	69	78	40	66	72	37
26 Sep 75	72	72	37	59	79	40
7 Nov 75	33	*	*	31	*	*

[1]Density expressed as the number of animals per ha. See text for an explanation of density calculation procedures.

*Not estimated.

TABLE 2. Pocket mice sex and age classes.

Date	Control Plot Total	Sex and Age Classes: Adults male	Adults female	Sub-Adults male	Sub-Adults female	Disposal Plot Total	Sex and Age Classes: Adults male	Adults female	Sub-Adults male	Sub-Adults female
1974										
May	37	15	22	0	0	6	3	3	0	0
May	35	17	18	0	0	14	9	5	0	0
Jun	26	11	8	5	2	16	10	3	2	1
Jul	35	10	10	9	6	26	8	2	7	9
Aug	49	5	8	21	15	30	6	0	12	12
Sep	60	3	8	33	16	43	4	2	19	18
Oct	72	3	6	39	24	53	1	2	25	25
Nov	69	0	3	39	27	40	1	1	20	18
Dec	16	0	1	8	7	11	0	0	8	3
1975										
Jan	5	4	1	0	0	0	0	0	0	0
Feb	9	9	0	0	0	7	7	0	0	0
Mar	50	50	0	0	0	34	34	0	0	0
Apr	79	48	31	0	0	59	30	29	0	0
May	52	28	24	0	0	43	23	17	1	2
Jun	50	17	15	9	9	57	14	15	19	9
Jul	62	10	10	26	16	64	9	13	28	14
Aug	69	2	5	35	27	66	0	10	30	26
Sep	72	0	5	41	26	59	0	5	37	17
Nov	33	0	0	22	11	31	0	0	21	10

Biomass

The weight of individuals within a population is also an indicator of general health and vigor. The average weight of adult pocket mice was calculated monthly for each plot. There were no significant weight differences within sex classes between control and the disposal plots. Generally, males showed a gradual increase in body weight from spring emergence until their disappearance from the trappable population with onset of winter torpor. The average weight of females increased during the period of reproductive activity, and decreased after the period when most were pregnant. The variability in subadult pocket mice caused by age differences obscures the significance of the weights in this age class.

Estimates of total live pocket mouse biomass per unit area (g/ha) are shown in Figure 2. These values were calculated by multiplying average biomass values for age and sex classes times the number of individuals represented in each class. Peak biomass values for the control and disposal study areas were 683 g/ha and 541 g/ha, respectively.

Home Range

Home ranges of pocket mice were estimated for both sex and age classes. The criterion for selection of animals was that each be captured at least seven times during the season

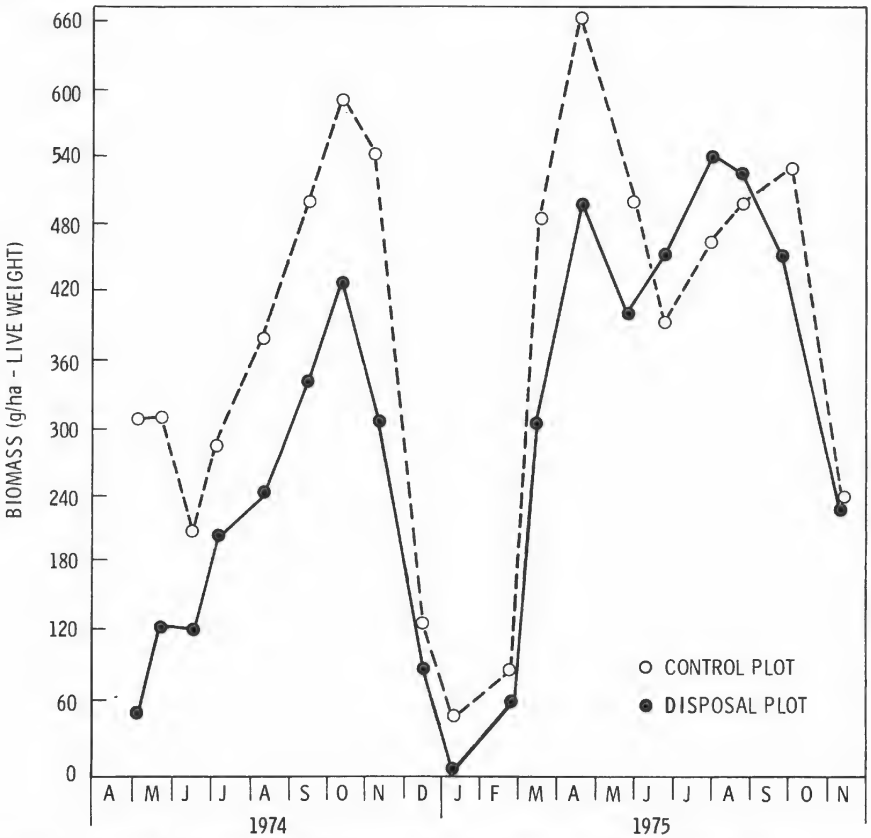

Figure 2. Seasonal biomass of pocket mice captured in Disposal and Control study areas.

of activity. The method described by Calhoun and Casby (1958) was used to calculate home ranges. This method calculates a circular home range within which the probability of the animal being found is 0.95. Estimates of home range are shown in Table 3. The home ranges of pocket mice on the control and B-C Cribs plots were within the range found in other studies in similar areas (O'Farrell *et al.*, 1975).

TABLE 3. Home ranges of **Perognathus parvus** (M^2).

	Control Plot				Disposal Plot		
	N	Mean	± S.E.		N	Mean	± S.E.
				1974			
Adult male	8	3125	± 666		7	3796	± 839
Sub-Adult male	17	1305	± 189		13	2304	± 446
Adult female	10	1446	± 263		2	1575	± 1165
Sub-Adult female	7	1265	± 334		10	907	± 79
				1975			
Adult male	24	1941	± 244		17	2151	± 261
Sub-Adult male	5	1186	± 356		16	1225	± 108
Adult female	10	746	± 105		12	958	± 187
Sub-Adult female	4	352	± 22		7	1060	± 335

Adults had larger home ranges than subadults in all cases but one, the exception occurring for adult and subadult females on the disposal plot in 1975. Estimates for subadult females also provide the only instance where the home range values for a sex and age class were larger in 1975 than that of the same class in 1974. A similar case occurred in 1974 with the subadult males: those on the disposal plot had larger estimated home ranges than did the subadult population occupying the control plot. Home ranges for subadults are difficult to analyze as new recruits are constantly in search of new home sites.

Discussion

The response of small mammals to ionizing radiation has been the object of extensive studies in the past (Dunaway *et al.*, 1969; French *et al.*, 1974; Gambino and Lindberg, 1964; Golley *et al.*, 1965; O'Farrell, 1969; O'Farrell *et al.*, 1972; and O'Farrell *et al.*, 1973). Questions continue to arise, however, concerning the impact of nuclear facilities on adjacent native wildlife populations. This assessment clearly shows that pocket mouse populations inhabiting areas adjacent to waste disposal sites and populations inhabiting control areas remote from radiation control zones to be equivalent in terms of abundance, sex ratio, reproductive condition, biomass, and home range.

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Size, Seasonality, and Sex Ratios of the Bay Pipefish (Syngnathus leptorhynchus) in Oregon

Abstract

Bay pipefish (*Syngnathus leptorhynchus*) captured in the Yaquina estuary, Oregon, ranged from 6.8 to 38.5 cm TL and from less than 0.2 to 20.3 g wet weight. Most (63 percent) pipefish weighed less than 1.5 g. Females were proportionately longer than males. The length-weight relationship was log W = −3.70 + 3.12 log TL (cm). The greatest observed density was 0.10 pipefish/m^2; densities were greater during daylight than darkness. The sex ratio prior to and during the breeding season was as great as 4 females:1 male for those longer than 17.0 cm TL, but apparently the sex ratio is inadequate to determine if males are ever in short supply. The breeding season extended from February to at least July. *Syngnathus leptorhynchus* were present throughout the year but were most abundant from December through May. In June, most pipefish emigrated away from the study area and may have moved up the estuary.

Introduction

Along the California coast there are at least four species of Syngnathidae (Miller and Lea, 1972), but along the eastern Pacific coast north of California only one species occurs, the bay pipefish (*Syngnathus leptorhynchus*) (Herald, 1941; Hart, 1973). Bay pipefish are found around wharves and eelgrass (*Zostera marina*) (Hart, 1973).

This study examines the length-weight relationships, densities, ages, and seasonal abundances of bay pipefish in a central Oregon coastal estuary, and compares the size, length of the breeding season, and sex ratios of these Oregon pipefish with those of California studied by Herald (1941).

Study Area and Methods

I conducted monthly sampling in the 15.8 km^2 Yaquina estuary, an inundated river valley located on the central Oregon coast (44° 38′N, 124° 03′W), from August 1975 through July 1976 and in January and February 1977. A beach seine designed to prevent rolling (Bayer, 1979) was used to capture pipefish in eelgrass at embayment areas 2-3 km from the mouth of the estuary in water 0.4-0.7 m deep. The seine was 3.0 m long and 1.1 m high with a 1.0 cm stretched mesh. Each sample was composed of a series of 10 hauls, each approximately 30 m long. A sample covered an area of approximately 600 m^2.

After capture, the total length of each fish and the wet weight of most fish were recorded. For those fish not weighed, a weight was estimated using a length-wet weight curve. In this paper, all length measurements are Total Length.

Seasonality—Males were distinguished by the presence of a brood pouch with lateral

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flaps; males were found throughout the year (Fig. 1). With one exception in October, all males seined from August to March were longer than 17.0 cm. In April, some smaller males (<17.0 cm) with brood pouches with rudimentary lateral flaps began to appear (Fig. 1). In June, the smallest male with a brood pouch (12.8 cm) was

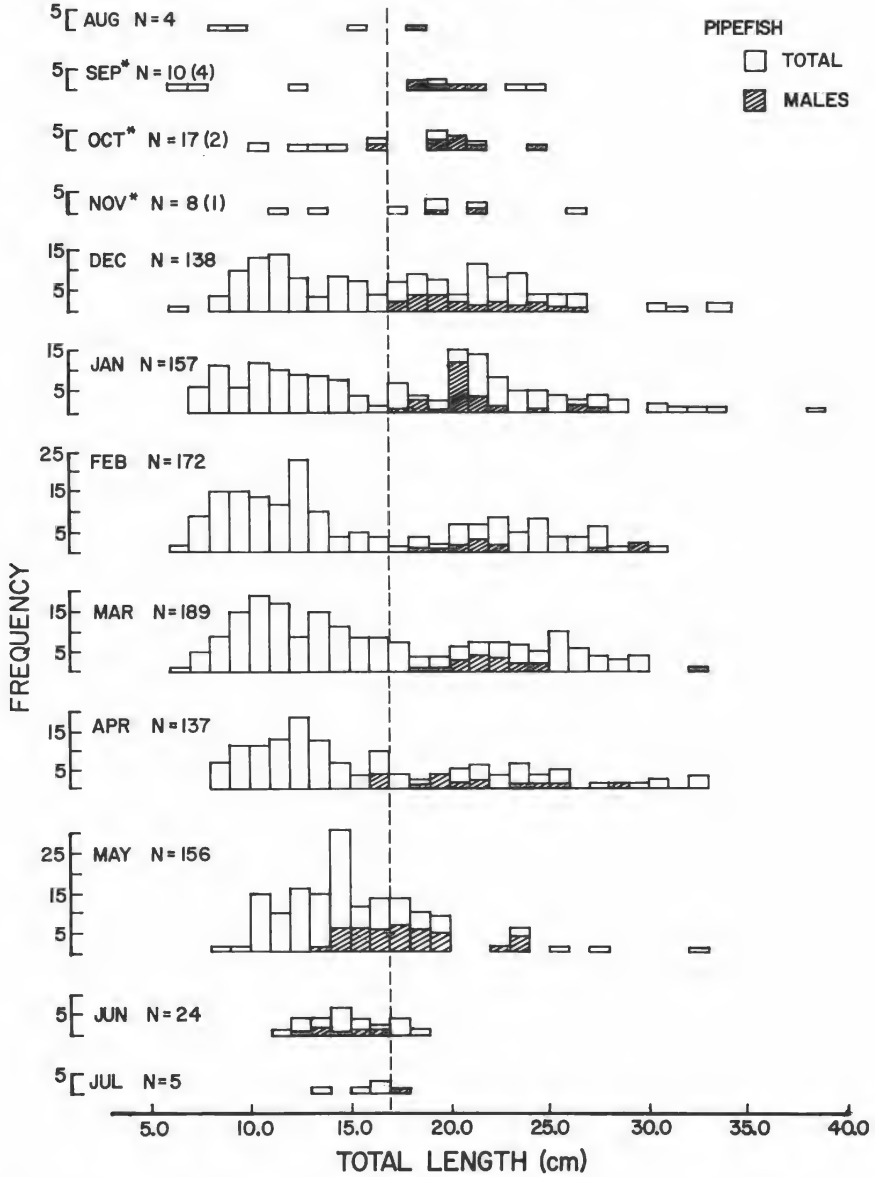

Figure 1. Length-frequency of pipefish. Number of samples in parentheses if different from five. Asterisk indicates night seines.

caught. Similarly, Herald (1941) found that brood pouch development for bay pipefish in California began at 11.0-14.0 cm, and that male bay pipefish in California began carrying eggs when 12.5-13.5 cm long. At the Yaquina estuary, the shortest male collected carrying young was 14.8 cm long in June.

The Yaquina estuary breeding season began in February when the lateral flaps of some males were observed to be semi-turgid. The first male carrying eggs was collected on 13 February 1976. This date is earlier than in British Columbia, where egg-carrying males were not found until the end of May (Hart, 1973). Egg-carrying males were still found in July at the Yaquina estuary, but not from August through January. At Netarts Bay, Oregon, males carrying eggs and embryos were found in June through September (Stout, 1976). In British Columbia, egg-carrying males have been found no later than August (Hart, 1973). In California, Herald (1941) found that the breeding season for bay pipefish at Point Mugu Lagoon extended throughout the year, with less reproduction from November through January.

Most pipefish (82 percent) were caught from December through May, just prior to and during the observed breeding season. Peak abundance occurred in March. In June there was a decrease of all sizes of pipefish (Fig. 1). In January and February 1977, the number of pipefish per sample was similar to that of January and February 1976, so the increase in pipefish abundance in winter was not limited to a single winter.

Size—A total of 1161 pipefish were collected; they ranged in length from 6.8 to 38.5 cm and in weight from less than 0.2 to 20.3 g. Although most pipefish (63 percent) weighed less than 1.5 g, only 27 percent of the total wet weight biomass collected (1.8 kg) was for fish weighing less than 1.5 g. Although few pipefish (7 percent) weighed more than 5 g, these contributed 25 percent of the total pipefish biomass.

The length-weight relationship (Fig. 2) was $W = -3.70 + 3.12 \log TL$ (cm) for 57 pipefish distributed evenly along the length range. Since only two pipefish longer than 34.0 cm were captured, the regression equation underestimates the weight of the largest pipefish (i.e., predicted 17.6 g, actual 20.3 g).

Although male and female pipefish of the same length weighed about the same (Fig. 2), a significantly greater proportion (30 percent) of the large females (>17.0 cm) were larger than 25.0 cm than for males (10 percent) (N=342♀, 145♂) (x^2=25.03, P<.01). Additionally, the largest female (38.5 cm, 20.3 g) was almost twice as heavy as the largest male (32.5 cm, 10.5 g). Herald (1941) did not report sexual dimorphism in size for bay pipefish, but females larger than males have been reported for other Syngnathidae, such as *S. floridae* (Gudger, 1905) and *S. typhle* (Heincke, 1880; cited by Breder and Rosen, 1966).

Five bay pipefish (all females) were longer than the greatest length previously reported (33 cm; Hart 1973). Body and tail ring counts for the two largest pipefish (38.5 and 37.8 cm) were 18 and 43, respectively, for both pipefish. X-ray analysis of the 37.8 cm female (Oregon State University Department of Fisheries catalogue no. 6354) revealed that the pipefish had 62 vertebrae. These measurements conform to those given for the bay pipefish in Miller and Lea (1972) and not to the kelp pipefish (*S. californiensis*) with which these large specimens may be confused on the basis of length. The kelp pipefish has been reported only as far north as San Francisco (Miller and Lea, 1972).

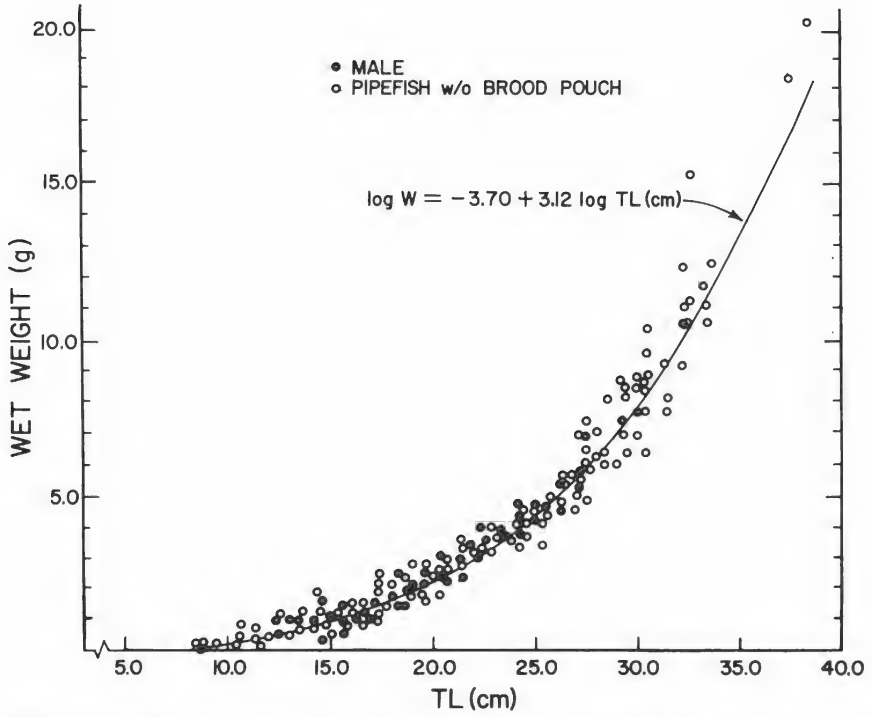

Figure 2. Pipefish length-weight relationship. Regression line calculated from measurements for 57 pipefish distributed evenly along the TL range.

Density—From December to May, when pipefish were most numerous (Fig. 1), the average density of pipefish per square meter was 0.05 (N=30 samples, range 0.02-0.10) with an average standing stock of 0.09 g/m^2 (range 0.01-0.20 g/m^2). Densities of *S. fuscus* have been found as great as 0.19 pipefish/m^2 (Adams, 1976). Densities appeared to be greater during daylight than darkness, since in December significantly more bay pipefish were seined during daylight than at night ($t=2.38$, $P<.05$).

Sex ratio—From December through May, the sex ratio of pipefish longer than 17.0 cm was significantly different from 1 female: 1 male ($P>.01$, proportions test, Tate and Clelland, 1957:51) (Fig. 3). The ratio of females to males was highest in February, when males carrying eggs were first observed. The ratio then was 4 females:1 male for all pipefish longer than 17.0 cm and 6:7:1 for pipefish longer than 22.0 cm. Herald (1941) also found a sex ratio favoring females of from 3:1 to 8:1 for bay pipefish in California.

Age—Length-frequency data for December through February (Fig. 1) suggest that at least three different age-groups can be differentiated, with modes at about 13, 18, and 22 cm. The growth rate or length at different ages has not been determined for bay pipefish, but Bigelow and Schroeder (1953) report that *S. fuscus*, which is similar in size to *S. leptorhynchus*, can grow to 7.0 cm within two months of hatch-

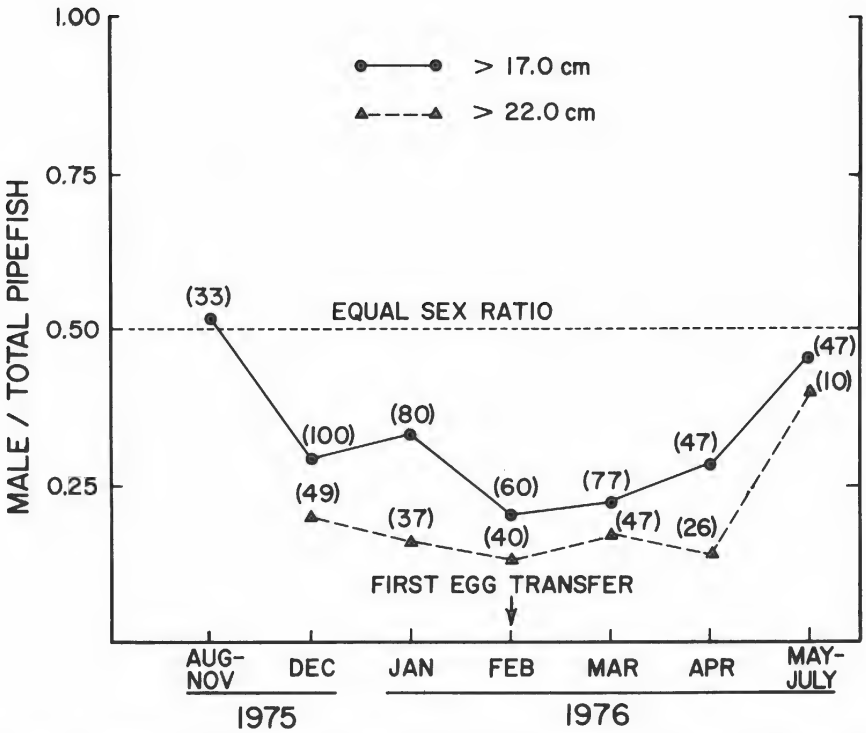

Figure 3. Proportion of all pipefish longer than 17.0 or 22.0 cm that are males. No proportion of males given for pipefish longer than 22.0 cm for August through November because fewer than 10 specimens were captured. Total pipefish examined are given in parentheses.

ing. Thus, the first mode (13 cm) may represent age group one, because pipefish hatched in the previous breeding season would be 6-12 months old in December through February.

The modes correspond to weights calculated from the weight regression of 0.6, 1.7, and 3.1 g, respectively. If the weight gain per year remained constant, approximately thirteen more years would be required before the weight of the largest pipefish (20.3 g) would be attained.

Discussion

In summer, pipefish may emigrate from the lower estuary to the upper estuary. Kate Myers (pers. comm.) indicated that pipefish were absent about 13.5 km from the Yaquina estuary mouth in winter, but present throughout most of the rest of the year. An intra-estuarine migration of pipefish may be related to seasonal salinity fluxes. The upper estuary is brackish in summer, with salinities of 15 to about 28°/oo compared to those of over 30°/oo in the lower estuary, but in winter salinities in the upper estuary may be below 20°/oo and are often 0°/oo, whereas the lower estuary has salinities over 25°/oo (Krygier and Horton, 1975). Thus, pipefish may remain

in water with salinities between marine and fresh water. Herald (1941) did not measure abundance nor indicate that an emigration of bay pipefish in California occurred.

Females are much more abundant than males during the breeding season in California (Herald, 1941) and at the Yaquina estuary. On theoretical grounds, Emlen and Oring (1977) predicted that females should be more numerous than males in species in which males incubate eggs. However, the operational sex ratio (i.e., the ratio of ripe females to males available to carry eggs; Emlen and Oring, 1977) is more appropriate in determining a biologically significant sex ratio rather than the simple sex ratio calculated by Herald (1941) and used in this study. But even the operational sex ratio may not be a valid means to determine if males available to carry eggs are ever in short supply because the number of males that a female will mate with at one time is unknown. In *S. leptorhynchus*, as in *S. floridae*, not all eggs are transferred to a male at the same time, and young at different stages of development can be found in the pouch of a single male (Herald, 1941; Gudger, 1905). Thus, a male may be less than wholly available to a female, and a male may mate with more than one female. Additionally, the number of males a female may mate with may be dependent on the size of the male, for in *S. leptorhynchus* (as in *S. schlegeli*) larger males can carry 4-6 times as many eggs as smaller males (Herald, 1941; Takai and Mizokami, 1959). An operational sex ratio thus only gives the ratio between whole animals, but in the case of pipefish, mating may not always be on a one female:one male basis. Therefore, more data than a simple sex ratio or an operational sex ratio are required to determine if males are ever in short supply.

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A Simplified Method for Evaluating Tides and Temperatures Affecting an Intertidal Insect on the Oregon Coast

Abstract

A simple model was developed to aid evaluation of the effects of tides and temperatures upon the distribution and biology of intertidal *Saldula fernaldi* Drake (Heteroptera:Saldidae). Incorporated are assumptions concerning the behavior of the insects and the major atmospheric and tidal variables affecting temperatures to which they are exposed. Developmental threshold temperatures determined in the laboratory correlated well with mean daily temperatures calculated by the model and the appearance of the various insect developmental stages in the field during the year.

Introduction

Intertidal plants and animals, submerged during high tides and exposed when the tide is low, are subjected to steep and variable gradients of environmental conditions. Not only does the elevation reached by each incoming tide vary, but diurnal and seasonal fluctuations of oceanic and atmospheric conditions make the specific environment for a given intertidal organism or community extremely complex. Collection of data by usual means, such as continuous recording of temperature, often presents considerable difficulties in a region which may be covered by several feet of water much of the day. Since many investigators do not have the technical support or expertise to undertake detailed, on-site data collection procedures during the initial stages of a study, they need a relatively simple way of determining if there is a correlation between observed organism response and selected environmental parameters.

This paper illustrates the development of such a simplifying analytical scheme. The principles of environmental modelling or simulation (Berryman and Pienaar, 1974) were used to simulate tide cycles and estimate temperatures affecting a population of the shore bug, *Saldula fernaldi* Drake (=*S. palustris* (Douglas)), inhabiting an estuarine salt marsh on the Oregon coast.

The Intertidal Environment

The fluctuating water level has a major influence on the distribution of most intertidal organisms. Along the Pacific coast of North America, tides are characterized by a marked difference in heights of consecutive high tides or low tides, a phenomenon called *diurnal inequality*. Instead of submergence or exposure times being related in a linear fashion to vertical elevation within the littoral zone, there are at times as much as two- or threefold differences in length of time submerged and exposed at locations within small vertical distances of each other. For example, a high low tide subjects organisms to a particularly long period of submergence between the preceding and following low tides, while a low high tide may leave them exposed for unusually

long periods of time between the preceding and following high tides (Doty and Archer, 1950). Doty (1946) correlated upper limits of certain algal zones with a critical level where maximum time of emergence from the water sharply increased, thus exposing the plants to desiccation and "sun-killing."

There are also changes in tide height associated with the spring to neap tide cycle. Cyclic changes in distribution of an intertidal staphylinid beetle have been correlated with such tidal rhythms (Craig, 1970).

When the intertidal region is submerged, organisms are subjected to many physical and chemical characteristics of the water. These characteristics include salinity, turbidity, and turbulence. Other factors to be considered in biological studies are layering of water temperatures, duration of submergence, and depth of water.

When the intertidal region is exposed, air temperature alone poorly defines the temperature of the specific microhabitat unless it is correlated with local factors such as wind, radiation, humidity, and various physiological adjustments and behavior patterns of the organism. Both night and day temperature extremes occur at the exposed surface (Lowry, 1969) near which many intertidal organisms live. Maximum and minimum soil surface temperatures and the time of their occurrence vary greatly, depending upon differences in cloud cover, wind, humidity, and so forth, from day to day. On cloudy days the temperature change from minimum to maximum is less because of reduced solar heat input and insulation provided by clouds. On sunny days, maximum soil surface temperature may be several degrees above air temperature. Minimum soil surface temperature, which occurs during the night, is generally lower than air temperature because of evaporation. Heat exchange then involves multiple paths of heat transfer between soil, air, and organism. For these reasons, and the fact that the insect population is exposed more than half the time, proper adjustment needed to render atmospheric temperature data relevant to the activities of the insects is a much more difficult process than dealing with water temperatures and tide information.

Methods

The following is a summary of assumptions made and subsequent steps taken to collect data which were then used to estimate tides and temperatures affecting the insects.

1. *Tidal elevation over time follows sine curves connecting high and low tide points* (U.S. Coast and Geodetic Survey, 1971) (Fig. 1). Tide levels recorded at Newport, Oregon, were corrected to the zero tide (MLLW or mean lower low water) reference level. Then tide times and heights at the study site were determined using U.S.C.G.S. (1971) locality corrections.

2. *The insects do not retreat before the incoming tide* (Stock and Lattin, 1976), *and they are submerged when the tide reaches the elevation where they live.*

A simple method was used to determine elevations of margins of insect distribution. The procedure was carried out during the time period between two consecutive tides, high to low, on a day when predictions showed that the tide would go from high to below zero level during daylight hours. Equipment included stakes, a watch, and a detailed map of the area drawn at a previous low tide on waterproof paper (including all features of biological interest and upon which elevation contour lines could be added). The method was as follows: (1) Exact time of high tide was noted and stakes

were driven at intervals along the water line. This line was mapped. (2) When the water line receded to a level of biological interest, the time was again noted and the water line staked and mapped. (3) Exact time of low tide was noted, the water line staked and mapped. (4) Each elevation (X) was calculated by substituting the time (T) at that elevation into equation 1 in Figure 1.

Using this technique, it was determined that the insects live between approximately 1.7 to 2.3 m (5.5 to 7.5 ft) above zero tide level. A value of 1.8 m (6.0 ft) was used to approximate the elevation of the insect population.

3. *The body temperature of the insects goes instantaneously to water temperature when they are submerged.* This assumption is based on the small size of the insects (see assumption 4 below).

4. *The body temperature of the insects is the same as soil surface temperature when*

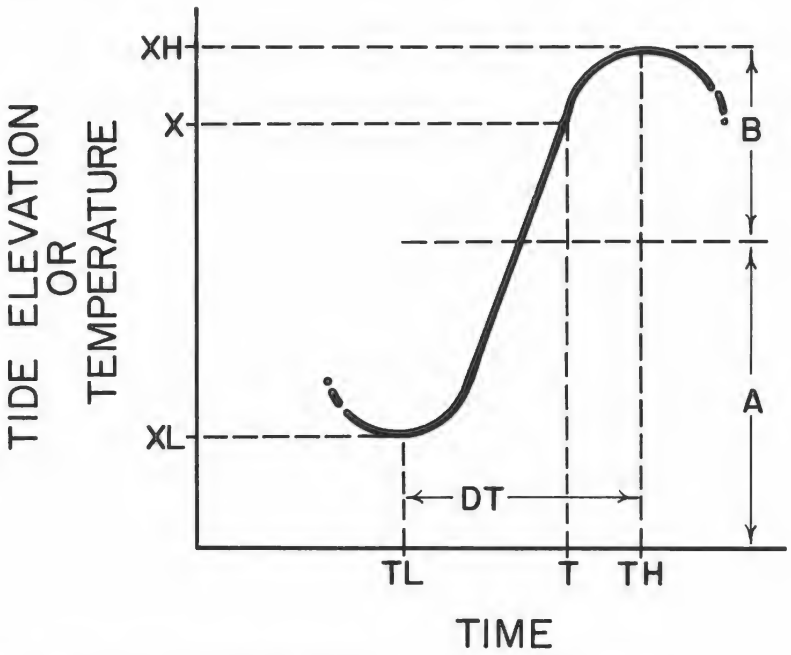

Figure 1. Method used to fit tide elevation or temperature data to a sine curve.

$$A = \frac{XH + XL}{2}$$

$$B = \frac{XH - XL}{2}$$

$$DT = TH - TL$$

$$X = A + B \sin \left[\frac{\pi}{DT}\left(T - \left(TL + \frac{DT}{2}\right)\right)\right] \qquad (1)$$

$$T = \frac{DT}{\pi} \arcsin \left(\frac{X - A}{B}\right) + TL + \frac{DT}{2} \qquad (2)$$

where XH = elevation of high tide or maximum temperature, XL = elevation of low tide or minimum temperature, TH = time of high, TL = time of low, X = elevation or temperature, and T = time.

they are not submerged. For many organisms, factors such as size, behavior, and color can create differences between body temperature and ambient temperature. However, for small insects (such as *S. fernaldi*) living close to the soil surface, where wind velocities approach zero, the influence of these factors on body temperature may be considered negligible (Digby, 1955).

5. *The body temperature of the insects goes instantaneously to soil surface temperature when the tide recedes from their level.*

6. *Soil surface temperature follows sine curves between a daily minimum one hour before sunrise and a maximum at noon* (Fig. 1). Maximum soil surface temperature was estimated by correlating soil surface and air temperatures measured at the study site on several days chosen to represent variable weather conditions with a variety of published and unpublished data. Data incorporated into the final estimate include maximum and minimum air temperatures recorded 0.5 km away in Toledo, Oregon, and radiation and precipitation data from the National Oceanic and Atmospheric Administration (1971 a, b, c), the Oregon State University Marine Science Center and the U.S. Coast Guard at Newport, Oregon. From these data, the highest correlation between Toledo air temperature and measured soil surface temperature was obtained by categorizing days according to radiation and precipitation levels and making general assumptions about the relation between air and soil surface temperature on different days during the year. For example, during winter months, soil surface maximum temperature was considered equal to air maximum on all days; in July, the soil surface maximum was set at up to 9°C higher than air maximum on very sunny days.

Minimum soil surface temperature was estimated by subtracting 1°C, the average difference between dry- and wet-bulb temperatures on the Oregon coast, from recorded air minimum temperatures.

The Model

The complete model calculated times of submergence and exposure of the insect population for each day (from which cumulative submergence and exposure periods were derived) and mean daily temperature. Input variables include:

1. Date;
2. Times and heights of high and low tides (THA, HHA, TLA, HLA, THB, HHB, TLB, HLB—where THA is the time of the first high tide, HHA the height of the first high tide, and so on);
3. Water temperature (DW);
4. Maximum soil surface temperature (DMAX);
5. Minimum soil surface temperature (DMIN);
6. Time of occurrence of minimum soil surface temperature (TMIN); and
7. Elevation (X) in meters above zero tide level of intertidal region of interest.

Calculation of mean temperature took place in five steps (Fig. 2). Data obtained in steps 1 and 2 formed the basis for calculation of cumulative periods of tidal submergence and exposure. Although there is a theoretical maximum of three separate submerged periods and four exposure periods for each day, Figure 3 illustrates a more common situation, three submerged periods and two exposed periods. In this example, elevation X was completely submerged during the early morning (time 0 to TMIN),

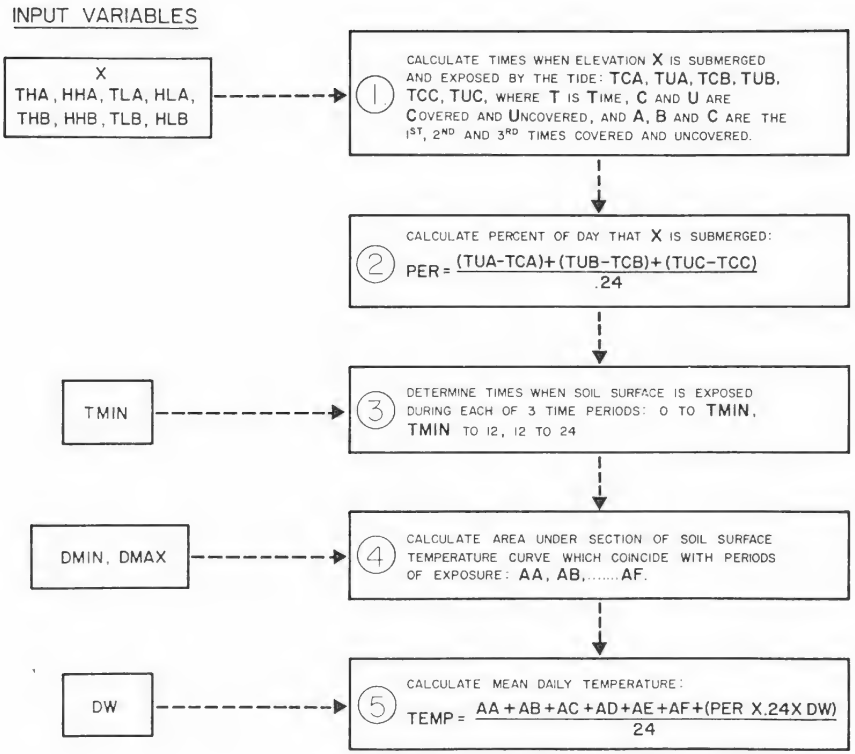
INPUT VARIABLES
X
THA, HHA, TLA, HLA,
THB, HHB, TLB, HLB
1
CALCULATE TIMES WHEN ELEVATION X IS SUBMERGED AND EXPOSED BY THE TIDE: TCA, TUA, TCB, TUB, TCC, TUC, WHERE T IS TIME, C AND U ARE COVERED AND UNCOVERED, AND A, B AND C ARE THE 1ST, 2ND AND 3RD TIMES COVERED AND UNCOVERED.
2
CALCULATE PERCENT OF DAY THAT X IS SUBMERGED:
PER = (TUA-TCA)+(TUB-TCB)+(TUC-TCC) / .24
TMIN
3
DETERMINE TIMES WHEN SOIL SURFACE IS EXPOSED DURING EACH OF 3 TIME PERIODS: 0 TO TMIN, TMIN TO 12, 12 TO 24
DMIN, DMAX
4
CALCULATE AREA UNDER SECTION OF SOIL SURFACE TEMPERATURE CURVE WHICH COINCIDE WITH PERIODS OF EXPOSURE: AA, AB,.....AF.
DW
5
CALCULATE MEAN DAILY TEMPERATURE:
TEMP = AA+AB+AC+AD+AE+AF+(PER X.24X DW) / 24

Figure 2. Flow diagram for estimation of mean daily temperature.

exposed part of the time interval TMIN to 12 (TMAX), and exposed two time intervals during the afternoon and evening, 12 to 24. The total submergence period during the day was 32 percent.

In calculating cumulative exposure and submergence periods for a given elevation, periods of tidal submergence or exposure extending to midnight were added to the corresponding periods of submergence or exposure starting at time zero the next day. Continuous submergence and exposure periods were calculated for 0.03 m (1.0 ft) increments from 1.2 to 2.6 m (4.0 to 8.5 ft) above zero tide level for each day between 1 April and 31 October 1971.

Mean daily temperature was calculated for each day of the year according to steps 3-5, Fig. 2. The complete model for determining mean daily temperature can be visualized as a tidal elevation curve superimposed on a soil surface temperature curve for each 24-hr calendar day (Fig. 4). The area under the soil temperature curve for periods when the soil surface was exposed was added to the product of water temperature and the total time in hrs that the elevation was submerged. This value was then divided by 24 hrs to obtain mean daily temperature. For the day illustrated in Figure 4, mean temperature was 17°C.

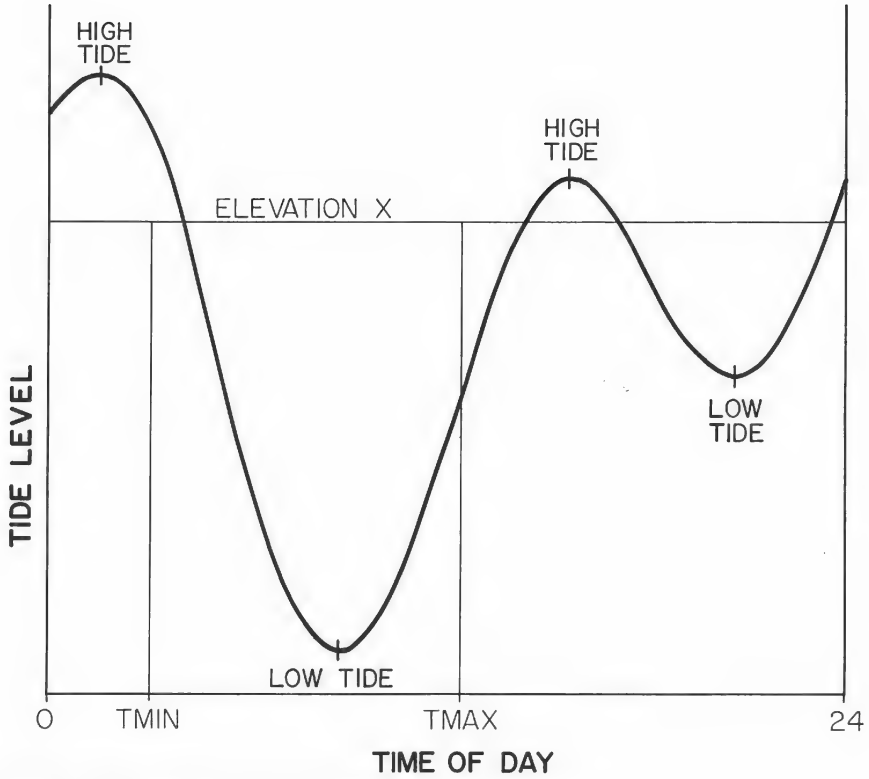

Figure 3. Tide elevation curve for a single day.

Results

Tidal submergence and exposure data are summarized in Figure 5. Maximum submergence time decreased sharply from 17 to 9 hrs between 1.4 and 1.5 m (4.5 to 5.0 ft) above zero tide. This critical level resulted from extremely high low tides which occurred several times during 1971. Specifically, low tides receded only to 1.5 to 1.4 m on 5 occasions between April and September. Since the insects live above the 1.5 m level, they were regularly submerged for up to 9 hrs at a time but not for longer periods. At about 2.0 m (6.5 ft), exposure periods increased abruptly from 24 to greater than 60 hrs at a time, although the insect population was uniformly dense up to the 2.3 m (7.5 ft) level.

Integration of water and soil surface temperatures revealed that temperatures affecting the insects are generally lower, and considerably more variable, than water temperatures over the year (Figs. 6, 7). However, comparison of the model-calculated temperatures with mean soil surface temperature alone (small circles in Fig. 6) show that the water has a moderating effect and acts to reduce fluctuations in temperatures affecting the insects from day to day.

Mean daily temperatures calculated by the model were compared to observations of the development of the insect in the field and under controlled temperatures in

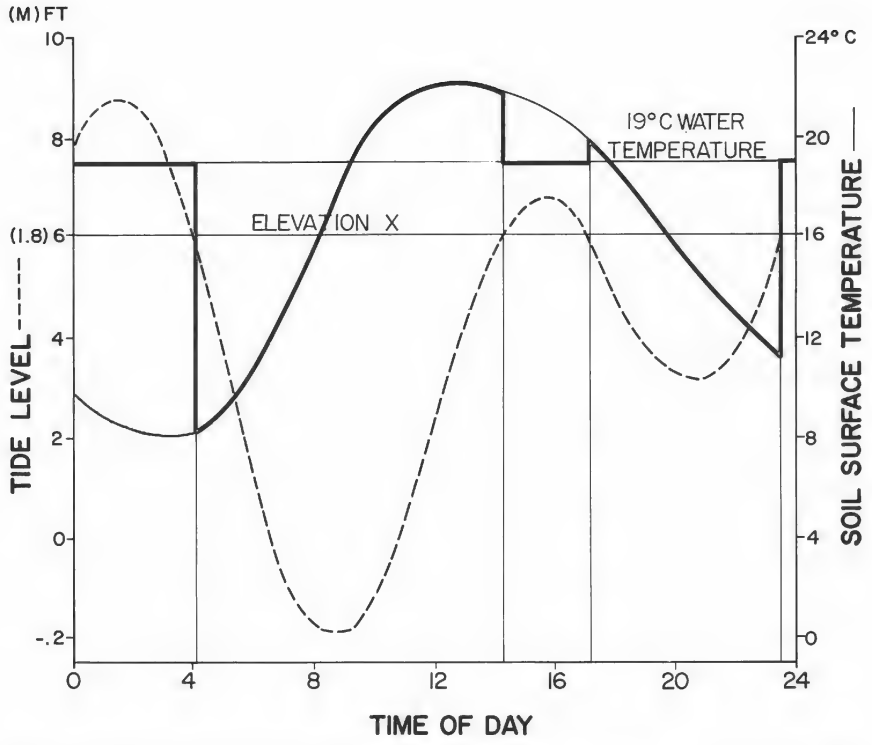

Figure 4. Superimposed curves of tidal elevation and soil surface temperatures for one day. Mean daily temperature at tide level 1.8 m (6 ft) equals total area under dark line divided by 24 hrs.

the laboratory (Figs. 6, 7). In laboratory growth chambers, the minimum temperature for embryonic development through hatching was 10°C, and a mean temperature of 15°C was required for development to the adult stage (Stock and Lattin, 1976). These threshold temperatures correlated well with mean daily temperatures calculated by the model and the appearance of the various insect developmental stages in the field during the year. The first nymphs appeared in April after about a month of mean daily temperatures fluctuating above 10°C. The first adults emerged after mean daily temperatures began to rise above 15°C. There was also a correspondence between decreasing mean daily temperatures in August and September with the end of reproductive activity (i.e., oviposition and mating). Mean daily temperatures of over 27°C were the upper limit for normal development and activity of these insects in controlled laboratory experiments. Calculated mean daily temperatures never exceeded 24°C.

When soil surface temperatures measured on 11 different days during April through September 1971 were compared to the temperatures predicted by the model for each day and time, the fit was unsatisfactory (d.f. $= 7$, $X^2 = 8.83$).

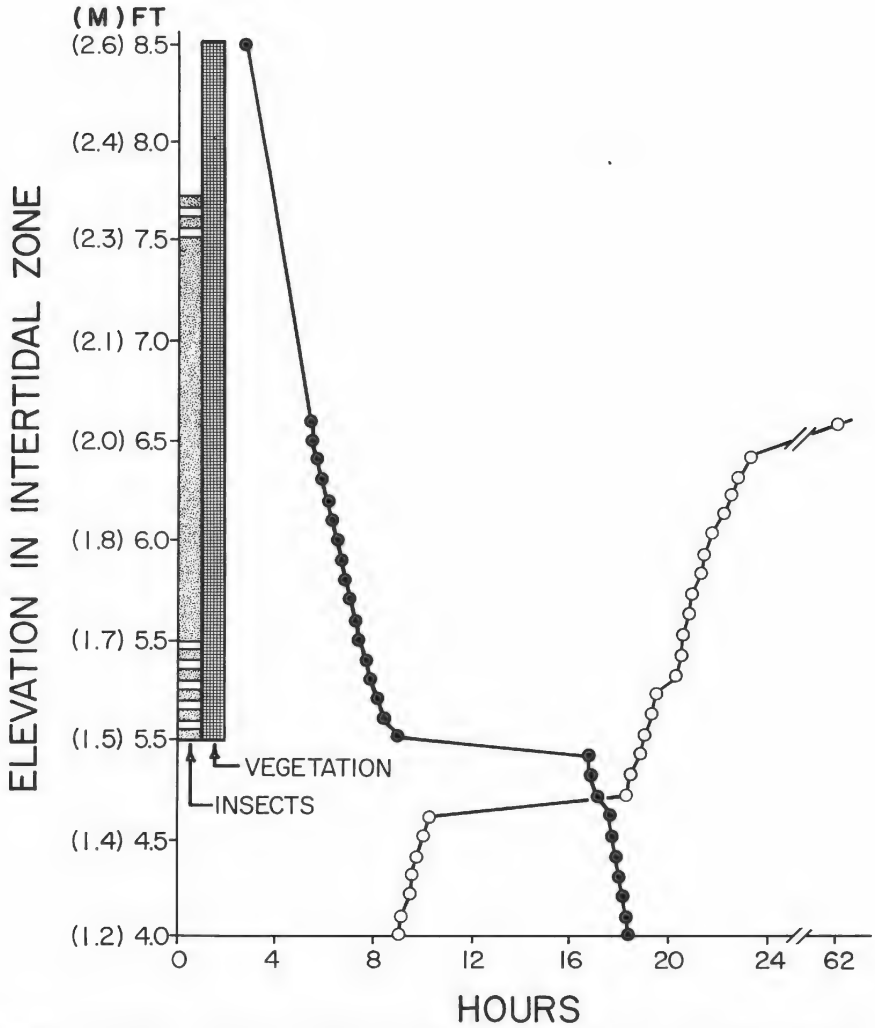

Figure 5. Duration of maximum continuous tidal submergence (dots) and maximum continuous exposure (circles) at successive elevations between 1 April and 31 October 1971. Vertical range of the insect populations and the salt marsh vegetation is indicated by vertical bars.

Discussion

This work shows that balance can be struck between data collection and the use of simplifying assumptions to build a descriptive model of the complex intertidal zone. Despite some apparently flagrant extremes of data simplification such as those defining soil surface temperature as a series of sine curves, a fixed time for maximum and minimum soil surface temperature, and the instantaneous change of the insect's temperature back to soil surface temperature when the tide receded, there was a reasonable

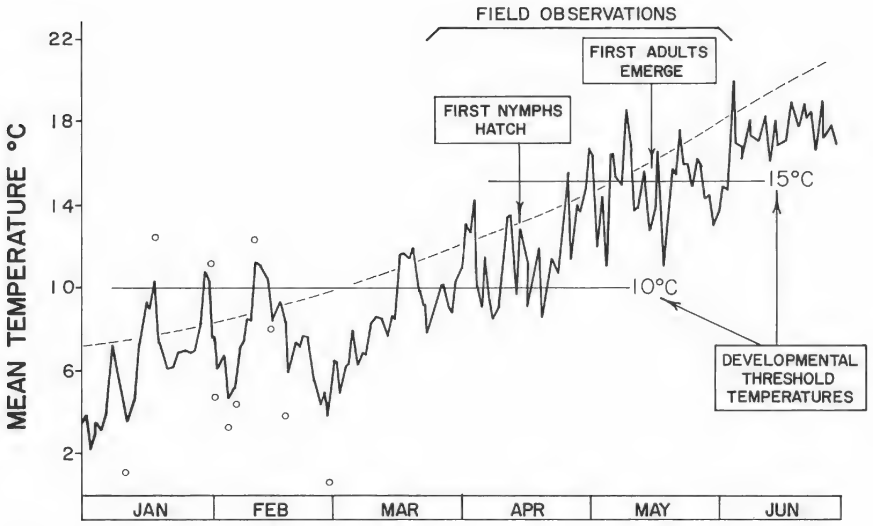

Figure 6. Life cycle events for *S. fernaldi* in relation to calculated mean daily temperatures of insects in the field, January to June 1971. Faint broken line is water temperature and circles are mean daily soil surface temperatures.

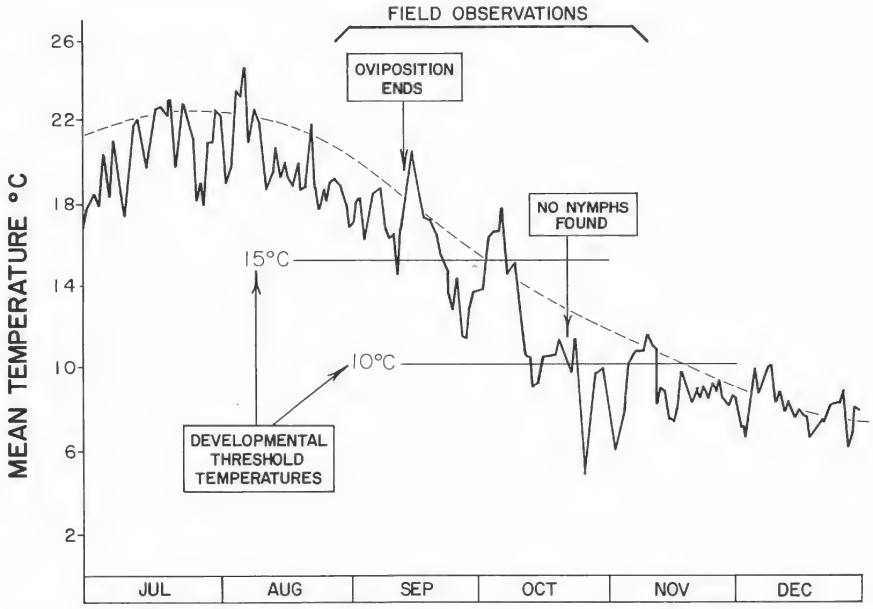

Figure 7. Life cycle events for *S. fernaldi* in relation to calculated mean daily temperatures of insects in the field, July to December 1971. Faint dotted line is water temperature.

correlation between calculated tide and temperature information and observations of insect distribution and development in the field and laboratory. Comparisons of model-calculated temperatures with soil surface and water temperatures alone revealed that actual temperatures to which the insects are subjected are more closely approximated by soil surface temperatures. This development is not unexpected, since the insects are only submerged about a third of the time. However, the model produces a much closer approximation of actual temperatures as it incorporates the moderating effect of the water in reducing fluctuations in temperatures affecting the insects.

These methods can serve as a base for biological studies of many types in the intertidal zone. Using an approach of this kind, important information on the distribution of intertidal animals and plants and their degree and mode of adaptation to various aquatic or atmospheric stress factors can be obtained. For example, the scheme can be modified to give the duration of continuous time intervals above or below a given temperature for tolerance or survival studies. Tidal submergence data can be used to assess the effect of changes in water level, turbidity, or temperature on the distribution or survival of organisms with specific requirements supplied by natural tidal rhythms.

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Sulfate Minerals in Snake River Plain Volcanoes

Abstract

Various species of sulfate minerals are found within the vent complexes of Holocene lava fields of the Snake River basalt province, Idaho. The identification of the minerals was surprisingly difficult owing to reversible hydration reactions which occurred spontaneously with minor changes in temperature and humidity. Those minerals identified include various hydrous sulfates of Na, Mg, Ca, and Fe. The locations of the deposits suggest a fumarolic origin; however, known phase stabilities of the sulfates prohibit high temperatures of formation. A hybrid origin with ground water reworking originally fumarolic deposits is suggested for these occurrences.

Introduction

Extensive deposits of various sulfate minerals have been found in a number of Holocene lava fields within the Snake River Plain basalt province in Idaho (Fig. 1). The sulfate minerals (gypsum, mirabilite, bassanite, thenardite, bloedite, epsomite and jarosite) were found in various combinations in sheltered areas in the flows, mostly in vent craters and lava tubes.

The first such deposit reported was from Craters of the Moon lava field (Stearns, 1963; Peck, 1974), where massive encrustations of mirabilite + gypsum and powdery deposits of jarosite were encountered at Crystal Pit, a spatter cone. Similar deposits were later found at Hell's Half Acre lava field in conjunction with other investigations (Karlo, 1977). The existence of these deposits was somewhat surprising, since evidence of fumarolic activity is generally lacking in Snake River Plain volcanoes. Subsequent but by no means exhaustive collections were made at each of the major Holocene lava fields, and they form the basis of this report.

An interesting aspect of these deposits is the inordinant difficulty involved in identifying the minerals present. Standard X-ray techniques for identification give aberrant results in that the X-ray patterns produced are often unrepeatable. These difficulties are attributed to hydration-dehydration reactions resulting from minor changes in ambient temperature and/or humidity.

Occurrences

The sulfates occur either as encrustations or as powdery deposits. Encrustations of compact masses of micro-crystals were found lining the walls and ceilings of lava tubes and other cavities at Hell's Half Acre, Wapi, and Shoshone lava fields (Fig. 1). These

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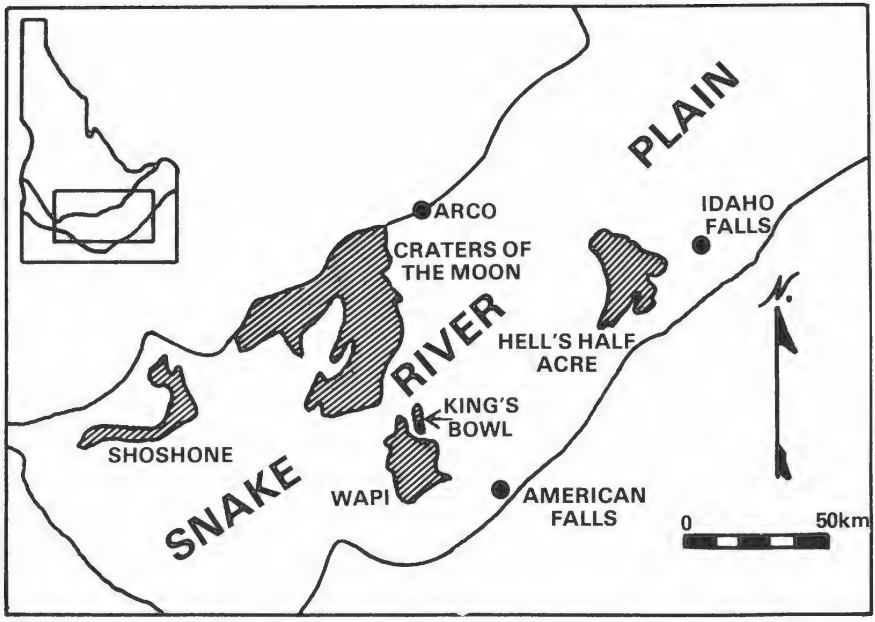

Figure 1. Locations of Holocene lava fields within the Snake River Plain, Idaho, from which sulfate minerals have been collected.

crusts vary considerably in thickness and extent; the most massive is 15 cm thick. Surfaces of the crusts are either globular, which is the original mode of occurrence, or, more commonly, rough with dissolution pits in areas affected by groundwater. The crusts were invariably found to be mixtures of gypsum + bassanite in contrast with the mirabilite + gypsum crusts reported from Craters of the Moon (Peck, 1974).

Powdery deposits were found at or near the vent areas of all the lava fields, and occur as layers on cavity floors, as fracture fillings, or less commonly as vesicle fillings. The layer deposits are typically discontinuous, show no stratification, and are 2-6 cm thick. All the powders are completely disaggregated and can easily be blown from their resting places. The powders are extremely fine-grained, with no crystal shapes discernible through a petrographic microscope. The minerals identified in the powders from each of the lava fields are: bloedite + thenardite, and bloedite + epsomite at Hell's Half Acre; thenardite and jarosite at King's Bowl, thenardite at Craters of the Moon; epsomite at Shoshone; and bloedite + epsomite at Wapi.

Identification

No effort was made to ensure that samples would not undergo phase changes prior to analysis owing to changes in temperature or humidity. All sample localities, while sheltered, were nevertheless freely exposed to the atmosphere, and any phase changes occurring subsequent to sampling would undoubtedly have occurred in the original environment.

The minerals were identified by X-ray diffraction and differential thermal analysis.

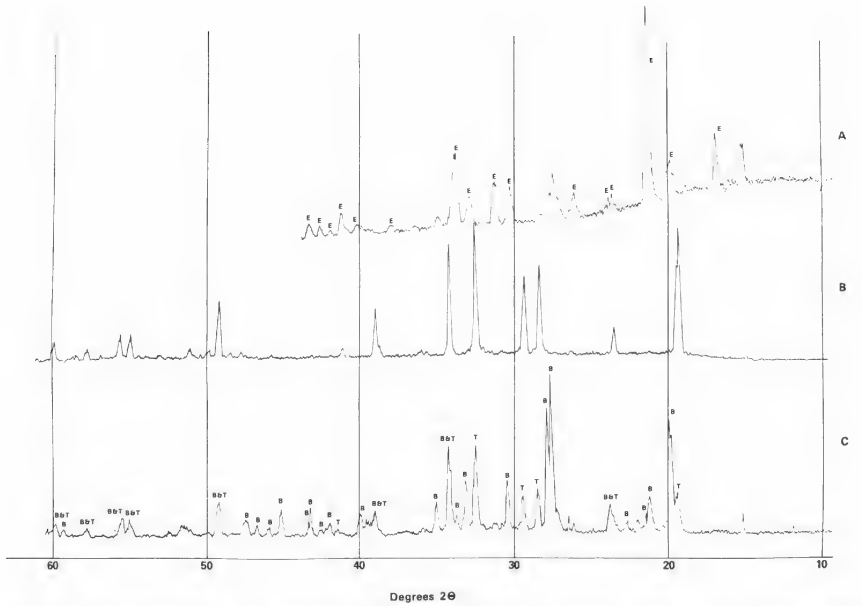

Figure 2. Representative X-ray powder diffraction patterns of sulfate deposits from Snake River Plain volcanoes. A. Epsomite (labelled E) from Pillar Butte, with unlabelled peaks representing a phase or phases which resulted from partial dehydration of the sample; B. Thenardite from King's Bowl; and C. Bloedite (B) and thenardite (T) from Hell's Half Acre.

X-ray diffraction powder analyses were done on a Phillips Norelco X-ray generator and chart recorder, with a goniometer speed of 1°/min., coupled with a chart speed of ½ in./min. The samples were prepared by settling the powders on a glass slide, using acetone as the wetting agent. Representative X-ray patterns are shown in Figure 2. Differential thermal analyses were also performed on selected samples, courtesy of Mettler Laboratories. The DTA results supported our X-ray identification of the sulfate phases.

Interpretation of X-ray patterns for samples containing epsomite was challenging since the epsomite readily undergoes hydration transition to hexahydrite (and vice versa) with minor fluctuations of room temperature or atmospheric humidity. Since the transitions rarely went to completion, various unidentified partial hydration stages occurred with the principal epsomite or hexahydrite phases. In several instances, the hydration states of the minerals apparently changed during the diffraction run, giving some highly puzzling patterns. Figure 2a shows a typical result for pure epsomite with some unlabelled, spurious peaks appearing in an otherwise simple pattern. Similar results were found with mixtures containing thenardite which formed small quantities of mirabilite on hydration. As an aid to identification, difficult samples were partially dehydrated by baking at 70°C for 24 hours, after which all erratic behavior disappeared. Baked unknowns were found to be simple mixtures containing the monohydrate form kieserite ($MgSO_4 \cdot H_2O$).

A similar circumstance was reported by Mitchell (1978). He found that pure

epsomite ($MgSO_4 \cdot 7H_2O$) progressively changed to hexahydrite ($MgSO_4 \cdot 6H_2O$) and starkeyite ($MgSO_4 \cdot H_2O$) on dehydration at room temperature. Likewise, hydration of starkeyite produced a progressive change back to epsomite.

The degree of crystallinity varied for the different minerals examined. Thenardite appeared to have the highest crystallinity, giving clear X-ray diffraction patterns with peaks readily identifiable down to intensities of 4 percent of the principal (100) peak. Epsomite and bloedite did not appear quite as well formed. They yielded broader, less intense peaks, with the peaks predicted for the shorter d-spacings absent or ill-defined. Jarosite commonly gave poorly defined patterns with only the principal peaks present, or in some samples, showed only the broad bulge pattern associated with amorphous material, not an uncommon characteristic of this mineral.

Origin

Peck (1974) hypothesized that the Crystal Pit deposits at Craters of the Moon were formed by groundwater leaching of the basalts followed by subsequent deposition when the water entered open cavities. Peck discounted the role of fumarolic activity since mirabilite has been reported elsewhere from non-volcanic environments. However, the extreme youth of these lava flows, 2000-4000 yrs. B.P. (Prinz, 1970; M. Kuntz, U.S.G S., pers. comm.), and the generally arid climate of southern Idaho are not in accord with this leaching hypothesis.

Stearns (1963) suggested that the sulfates were fumarolic in origin, which seems a more likely hypothesis; but mineralogic data do not fully support this. Jarosite precipitates at a temperature of about 110°C (Fairchild, 1933), which is well in the range of fumarolic activity. However, in the system Na-Mg-SO_4-H_2O, bloedite forms in equilibrium with epsomite and mirabilite between 20.6°C and 70°C at 1 atm. (Doelter, 1926), and the transition of mirabilite to thenardite in the $Na_2SO_4 \cdot H_2O$ system occurs at approximately 32°C (Hill and Wills, 1938). These minerals appear to have formed within temperature ranges well below that expected for fumarolic deposits.

Peck (1974) may have been correct in stressing the role of groundwater, but its primary role in the Snake River Plain is more likely one of erosion (solution) rather than deposition. The sulfates are commonly present in the youngest flows but are absent from the older flows which have had longer exposure to groundwater. Although the deposits are extensive, they are not ubiquitous and are notably lacking in the wettest portions of lava caves. Further, the crust deposits show clear evidence of dissolution. Of the identified minerals, thenardite, epsomite and bloedite are soluble in water, and all of the minerals found are soluble in acidic solutions. None of the environments where the sulfates occur are fully protected from infiltrating water, and it is probable that the sulfate deposits are steadily diminishing in extent due to solution, rather than being actively deposited.

A "compromise" hypothesis seems most likely: an original series of deposits were fumarolic in origin, and the Jarosite powders and gypsum + bassanite crusts are the only remaining examples of this primary deposition. More soluble minerals were affected by groundwater and underwent solution, leaching, transport, and redeposition to varying degrees and in various combinations. The sulfates of Na and Mg are thus secondary minerals formed by reworking of the primary fumarolic deposits.

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A Comparison of Small Mammal Populations Occupying Three Distinct Shrub-Steppe Communities in Eastern Oregon[1]

Abstract

This study compares population parameters of small mammals occupying three distinct shrub-steppe communities in eastern Oregon. Pocket mice (*Perognathus parvus*) were found to be the dominant animals in terms of both biomass and density in cheatgrass (*Bromus tectorum*) and needle-and-thread grass (*Stipa comata*) communities. Kangaroo rats (*Dipodomys ordii*) dominated a sagebrush-juniper (*Artemisia tridentata-Juniperus occidentalis*) community. Deer mice occurred in all study areas but were only abundant in the sagebrush-juniper community.

Introduction

This study compares population parameters of small mammals inhabiting three distinct plant communities within the shrub-steppe region of eastern Oregon. These data were gathered as part of an ecological assessment of a proposed electrical power generation complex (Rogers *et al.*, 1975). Current plans call for construction of a 550,000 megawatt coal fired generator. Nuclear generators may be added to the complex at a later time. Field data gathering sessions were conducted during 1973 and 1974.

Study Area

The study area is located about 19 km (12 mi) southwest of Boardman, in Morrow County, Oregon. Plant communities are typical of steppe communities in the semi-arid regions east of the Cascades. In the absence of recent fire, the plant communities are dominated by a shrub overstory. An understory comprised of herbaceous plants extends beneath and among the shrubs, with grasses being the important biomass contributors. The abundant shrubs are big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*). The important understory grasses are needle-and-thread (*Stipa comata*), Sandberg's bluegrass (*Poa sandbergii*), and cheatgrass (*Bromus tectorum*). Indian ricegrass (*Oryzopsis hymenoides*) and thick-spiked wheatgrass (*Agropyron dasystachyum*) are locally abundant on sandy soils. Three distinct plant communities were selected for study: one supports clumps of needle-and-thread grass, another swards of cheatgrass, and a third supports woody vegetation, especially big sagebrush and western juniper.

The climate of the area is characterized by hot dry summers and cold winters, with most of the precipitation occurring during fall and winter months. Precipitation

[1]Prepared for the U.S. Department of Energy under Contract No. EY-76-C-06-1830.

averages less than 25 cm (10 in) per year. The prevailing winds are westerly and may be occasionally strong.

The relative abundance of small mammals was studied by trapping, using a live-trap, mark, and recapture technique. Three grids of 144 traps each were established within cheatgrass, needle-and-thread grass, and sagebrush-juniper communities. The traps were arranged in a 12 x 12 grid pattern with 15 m intervals between traps. Each trap was placed inside a slightly larger metal box so that only the trap opening was exposed. The extra shielding helped to protect captured animals from extreme temperatures; in addition, a sheet metal tent was placed over the metal box and trap, preventing the sun's direct rays from overheating confined animals. Care was taken to visit the traps as early in the morning as possible during periods of hot weather.

Beginning in April 1973, all traps were opened for a total of 10 trapping sessions, ending in September 1974. The first seven sessions occurred at approximately monthly intervals. Additional sessions were conducted during February, June, and September of 1974. Only the cheatgrass community was trapped during June and September of 1974. Traps were provided with a sufficient quantity of seeds to prevent torpor in trapped animals. Traps were opened in late afternoon of the first trapping day and remained open for three successive days of trapping. A small quantity of mixed oatmeal and peanut butter was placed in the trap entrance as bait.

All captured animals were marked for individual identification by a series of toe amputations, weighed, determined as to sex, examined for reproductive condition, and released near the point of capture. Field data were recorded in notebooks and later transcribed to keypunch forms for computer processing.

Results and Discussion

Four species of small mammals were trapped on the three intensive study plots: Great Basin Pocket Mouse (*Perognathus parvus*), Deer Mouse (*Peromyscus maniculatus*), Ord kangaroo rat (*Dipodomys ordii*), and the Northern Grasshopper Mouse (*Onychomys leucogaster*).

The trap catches for the three study areas are shown in Tables 1 and 2. The numbers represent the total number of individuals captured during each trap session, thereby providing an indication of the abundance of animals of each species living

TABLE 1. Number of small mammals captured.

Species	Apr	May	Jun	Jul	Aug	Oct	Nov	Feb	Jun	Sep
Cheatgrass Plot										
Pocket Mouse	80	67	86	87	102	18	1	8	28	8
Deer Mouse	7	0	0	0	0	0	0	0	0	0
Grasshopper Mouse	0	0	0	0	0	0	0	0	0	0
Kangaroo Rat	0	0	0	0	0	0	0	0	0	0
Needle-and-Thread Grass Plot										
Pocket Mouse	43	70	92	93	81	8	3	8	not	
Deer Mouse	6	3	3	0	0	4	6	11	trapped	
Grasshopper Mouse	0	0	0	1	0	0	0	0		
Kangaroo Rat	0	0	0	0	0	0	0	0		
Sagebrush-Juniper Plot										
Pocket Mouse	21	29	25	20	18	5	0	2	not	
Deer Mouse	27	26	18	11	11	9	7	5	trapped	
Grasshopper Mouse	0	0	0	0	0	0	0	0		
Kangaroo Rat	25	34	25	31	29	36	37	30		

TABLE 2. Small mammal biomass.[1]

Species	Apr	May	Jun	Jul	Aug	Oct	Nov	Feb	Jun	Sep
Cheatgrass Plot										
Pocket Mouse	1344	1079	1340	1314	1509	223	12	108	473	121
Deer Mouse	109	0	0	0	0	0	0	36	0	0
Grasshopper Mouse	0	0	0	0	0	0	0	0	0	0
Kangaroo Rat	0	0	0	0	0	0	0	0	0	0
Needle-and-Thread Grass Plot										
Pocket Mouse	701	1120	1444	1432	1206	109	39	118	not	
Deer Mouse	109	43	42	0	0	66	110	210	trapped	
Grasshopper Mouse	0	0	0	0	0	0	0	0		
Kangaroo Rat	0	0	0	0	0	0	0	0		
Sagebrush Juniper Plot										
Pocket Mouse	336	432	380	302	275	64	0	30	not	
Deer Mouse	437	424	270	157	169	161	142	102	trapped	
Grasshopper Mouse	0	0	0	0	0	0	0	0		
Kangaroo Rat	1245	1703	1200	1473	1418	1804	1790	1605		

[1]Biomass expressed as grams (wet weight).

on each plot. Biomass values are expressed in terms of grams (wet weight) and represent an estimate of total biomass per species for each study plot.

The pocket mouse dominates both cheatgrass and needle-and-thread grass plots, accounting for 98 percent and 92 percent of individuals captured on the respective plots. Pocket mice accounted for only 25 percent of the individuals on the sagebrush-juniper plot. Pocket mice comprised over 90 percent of the total small mammal biomass on cheatgrass and needle-and-thread grass plots, but only 13 percent on the sagebrush-juniper plot. The decline of pocket mice in the trap catches during the early fall months is normal. They spend the summer months actively feeding and storing seeds. They remain largely below ground in burrows during the winter months and re-emerge as the weather warms in spring (O'Farrell *et al.*, 1975.).

Kangaroo rats require a sandy area in which to dig, as well as an abundant seed supply. These conditions, while satisfied in the sagebrush-juniper area, apparently preclude their inhabiting the other study sites. The kangaroo rats account for about half of the individuals captured in the sagebrush-juniper community (51 percent).

Deer mice were trapped on all study sites, but occurred in small numbers on the cheatgrass and needle-and-thread grass plots. The absence of deer mice from trap catches in mid-summer on these two plots was expected, as similar results were obtained in studies conducted on the Arid Land Ecology Reserve near Richland, Washington. There, deer mice were also often absent from mid-summer catches, although the cause for absence is not known. A single northern grasshopper mouse was captured on the needle-and-thread grass plot during July. These mice occur throughout the arid and semi-arid regions of the west, but at low densities (O'Farrell *et al.*, 1975).

Calculated sex ratios for pocket mouse populations averaged about 50 percent females in the cheatgrass and needle-and-thread grass plots, but only 36 percent in the sagebrush-juniper plot. Sex ratios of deer mice ranged from a low of 39 percent females on the needle-and-thread grass plot to 41 percent on the sagebrush-juniper plot and 44 percent on the cheatgrass plot. The kangaroo rat population averaged 38 percent females in the sagebrush-juniper study area. There were consistently more male kangaroo rats caught than females during all trapping sessions.

The small mammal abundance, biomass, and sex ratio data presented here provide

baseline information permitting a later evaluation of population changes related to the construction and operation of the power complex planned for northeastern Oregon.

Acknowledgments

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Phenology of Shrubs on a North Idaho Elk Range[2]

Abstract

A calendar of major phenological events for 12 species of shrubs is presented. Initiation of phenological events followed a predictable sequence among species, whereas the duration and completion of each event did not follow a consistent pattern. Year-to-year variations in phenology were related to climatological measurements.

Introduction

A shrub community commonly replaces conifers following logging and/or burning in the mountains of north Idaho. These seral brushfields are important for big game animals such as elk (*Cervus elaphus nelsoni*), deer (*Odocoileus* spp.), cougar (*Felis concolor*), and black bear (*Ursus americanus*), and many other species of smaller mammals and birds. The livelihood of numerous animal species depends upon proper management of these areas. Since the mid-1960s, research has documented the importance of seral brushfield communities and has found ways to enhance them with prescribed burning (Leege, 1968).

Many research and management activities associated with these seral shrub ranges need to be correlated with shrub phenology. Research has shown that the stage of plant development at which various rehabilitation treatments are conducted can influence their outcome (Hickey, 1971; Leege and Hickey, 1971). Management activities such as measuring browse utilization, counting pellet groups, slashing, prescribed burning, and seed collection need to be performed at the proper phenological period.

Few phenological studies have been conducted in north Idaho. Drew (1967) studied the phenology of a young seral shrub community. Phenological studies of coniferous species were conducted by Daubenmire (1949), and Bingham and Squillace (1957). Goyer (1966), Ollieu (1963), and Stephenson (1965) correlated phenological records with insect activity. Flowering dates of some angiosperms were presented by Marshall (1966). However, a phenological calendar of the type needed for brushfield research and management was lacking. This study was initiated to obtain such a calendar for some major shrub species in north Idaho and to evaluate the year-to-year variability as related to weather.

Methods

A study area was established in a seral brushfield on a southwest aspect at 640 m

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[2]A contribution from Idaho Federal Aid Project, W-160, Elk Ecology.

elevation in the Pete King Creek drainage. Pete King Creek is a tributary to the Lochsa River within the Clearwater National Forest (Fig. 1). This seral brushfield was created when a mixed conifer forest was eliminated by a wildfire in 1934. Soils on the area are derived from granitic bedrock of the Idaho Batholith and belong to the Jughandle or closely related soil series (Hickey, 1971). Vegetation is typical of the Cedar/Pachistima habitat type as described by Daubenmire and Daubenmire (1968). Weather follows a pattern of cool, rainy springs; hot, dry summers; cool, rainy falls and snowy winters with moderate temperatures. January has the highest

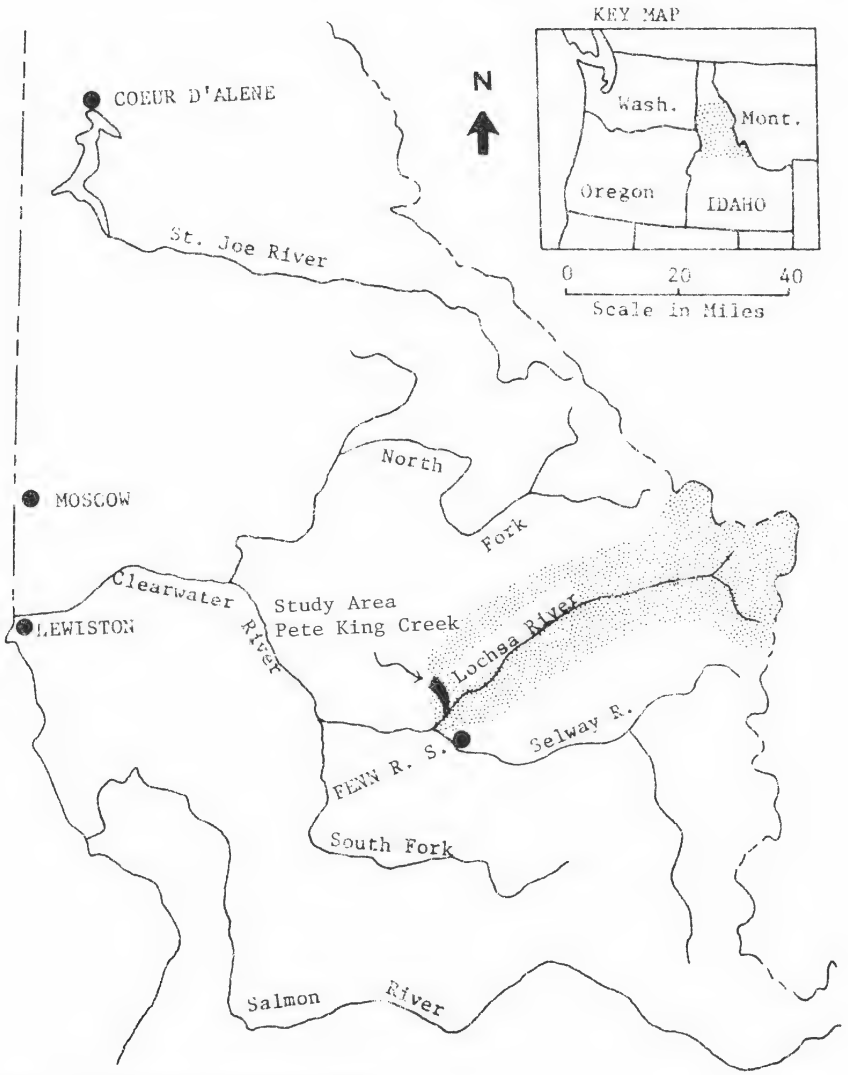

Figure 1. Area map of north-central Idaho.

TABLE 1. Weather records from Fenn Ranger Station, 1971-73.[1]

Year	JANUARY Temp. Max./Min.	JANUARY Precip.	FEBRUARY Temp. Max./Min.	FEBRUARY Precip.	MARCH Temp. Max./Min.	MARCH Precip.	APRIL Temp. Max./Min.	APRIL Precip.	MAY Temp. Max./Min.	MAY Precip.	JUNE Temp. Max./Min.	JUNE Precip.
1971	1.7/–3.3	21.0	6.0/–2.3	7.6	8.6/–1.3	11.6	15.2/1.0	8.9	22.4/5.4	9.0	22.6/7.7	10.5
1972	0.8/–6.1	14.7	4.2/–3.5	17.6	11.1/0.5	14.5	13.1/0.8	13.1	—/—	6.5	25.7/9.5	6.6
1973	1.2/–6.5	6.4	6.9/–3.8	4.8	11.0/–0.9	7.0	16.3/1.1	3.3	23.4/3.9	5.1	24.0/7.5	8.2
Long-term Average[3]	–1.6	10.7	1.8	8.3	4.4	8.7	9.1	9.3	13.5	8.6	17.1	8.0
	JULY		AUGUST		SEPTEMBER		OCTOBER		NOVEMBER		DECEMBER	
1971	30.9/8.9	0.9	34.2/9.4	0.8	21.6/4.3	4.9	14.8/1.0	7.5	6.0/0.0	9.3	1.7/–3.6	12.0
1972	30.9/10.2	3.4	32.9/10.8	2.5	22.1/4.0	6.2	16.7/2.2	4.2	8.1/–1.7	5.4	–0.2/–7.8	15.4
1973	32.5/9.4	0.2	32.8/9.3	0.5	23.6/5.8	7.7	15.6/1.0	7.5	4.9/–2.3	20.1	3.8/–2.7	15.4
Long-term Average[3]	21.5	1.9	21.1	3.1	16.0	5.6	9.7	7.8	3.7	10.8	0.0	10.9

	Annual Precipitation	Average Annual Temp.
1971	104.0	8.9
1972	110.1	—
1973	86.2	9.1
Long-term Average[3]	93.7	9.7

[1]U.S. Dept. of Commerce (1971-1973).

[2]Temperature is in °C and precipitation in cm.

[3]U.S. Dept. of Commerce (1976).

average precipitation and July the lowest. Average annual precipitation for the three years of this study was 100 cm at the Fenn Ranger Station, 14.5 km south of our study area at an elevation of 483 m (Table 1) (U.S. Dept. Commerce, 1971-1973).

Phenological information was obtained from twelve of the major shrub species usually associated with north Idaho seral plant communities: Rocky Mountain maple (*Acer glabrum*),[1] saskatoon serviceberry (*Amelanchier alnifolia*), redstem ceanothus (*Ceanothus sanguineus*), Pacific dogwood (*Cornus nuttallii*), red osier dogwood (*Cornus stolonifera*), creambush oceanspray (*Holodiscus discolor*), syringa or mock-orange (*Philadelphus lewisii*), mallow ninebark (*Physocarpus malvaceus*), bitter cherry (*Prunus emarginata*), cascara (*Rhamnus purshiana*), scouler willow (*Salix scouleriana*), and common snowberry (*Symphoricarpos albus*). For each of the 12 shrub species, three individual plants were selected and marked with metal tags for future location. Each plant selected was an average specimen without noticeable disease, insect damage, or defects. Ten qualitative measurements of phenological events were recorded for each individual plant for three summers beginning in 1971 (Table 2). These measurements were usually made at weekly intervals; therefore, each phenological event occurred during the week prior to the recorded date.

Results

A summary of the major phenological activities is contained in Table 3. Fairly consistent patterns existed among the 12 shrubs for the leaf emergence (Fig. 2). Oceanspray, syringa, snowberry, and ninebark were always the first species to initiate leaves be-

TABLE 2. Qualitative and quantitative measurements of phenological events.[1]

Phenological Event	Description	How measurement was made
Bud swell	The date on which majority of buds are enlarged but still within their winter scales.	General observation of entire plant.
Bud burst	The date on which a majority of the buds expose the green of new leaves from between the winter scales.	" "
Leaf emergence	The date on which the first leaves have straightened out from the twisted form they had in the bud.	" "
Full leaf	The date on which a majority of the leaves have attained full size.	" "
Stem elongation	The date on which branches start growth and cease growth, as determined by quantitative measurement.	Two twigs on each individual plant were flagged and measured.
Start of bloom	The date on which the first flowers open and expose the stamens and pistils.	General observations of entire plant.
Cease bloom	The date on which all flowering has ceased.	" "
Fruit development	The date on which the fruit begins (ovary enlargement) and ceases (maturity) enlargement.	" "
Change in leaf color	The date on which foliage begins and ceases to change from its summer color.	" "
Beginning leaf fall	The date on which the shrubs begin to shed their leaves.	" "

[1]Drew, 1967.

[1]Common and scientific names follow Asherin (1973). Binomial common names have been shortened in the remainder of the article (e.g., saskatoon serviceberry = serviceberry).

TABLE 3. A summary of major phenological activities of 12 north Idaho shrubs.[1]

Species	Year	Bud Swell[2]		Leafing Out		Stem Elongation		Blooming		Fruit Development[3]		Change in Leaf Color	Leaf Fall
		Begin	End	Begin	End	Begin	End	Begin	End	Begin	End		
Bitter Cherry	1971	—	4/27	5/4	5/19	5/19	7/14	5/4	5/19	5/26	8/25	9/30	9/30
	1972	—	4/28	5/6	5/27	5/27	7/3	5/19	5/27	6/2	8/12	9/26	9/26
	1973	4/15	5/2	5/2	5/28	5/28	7/12	5/11	5/28	5/28	8/10	10/2	—
Cascara	1971	—	4/27	5/4	5/19	5/11	7/21	5/26	6/9	6/18	—	9/30	—
	1972	4/19	5/6	5/6	6/2	5/19	7/12	5/27	6/13	6/20	—	10/9	—
	1973	—	4/23	5/2	6/4	5/2	7/4	5/28	6/12	6/19	—	10/2	—
Rocky Mtn. Maple	1971	—	4/27	5/4	5/19	5/11	8/25	5/4	5/26	6/2	—	9/30	10/8
	1972	—	4/28	5/6	5/27	5/12	8/1	5/6	5/27	—	8/1	10/9	10/9
	1973	4/3	4/23	5/2	5/16	5/9	6/26	5/2	5/16	—	8/3	10/2	10/2
Ninebark	1971	—	—	4/21	5/11	5/4	6/18	5/26	6/18	6/18	—	9/23	9/23
	1972	—	—	4/19	5/27	5/6	6/13	5/19	6/13	6/13	—	9/26	9/26
	1973	4/3	4/15	4/23	6/4	5/2	6/4	5/28	6/12	6/19	—	8/28	10/2
Oceanspray	1971	—	—	4/21	5/11	5/11	6/9	7/8	7/21	7/21	—	9/23	9/23
	1972	—	4/20	4/19	5/27	5/12	7/3	7/3	7/25	8/1	8/30	9/26	9/26
	1973	—	4/10	4/14	5/28	5/9	6/26	7/4	7/23	8/3	—	10/2	10/2
Pacific Dogwood	1971	—	4/27	5/4	5/19	5/19	6/24	5/4	5/19	6/9	8/25	9/23	10/8
	1972	—	4/28	5/6	5/26	5/19	7/25	5/27	6/13	6/13	8/30	9/26	—
	1973	4/3	5/2	5/9	6/4	5/16	7/12	5/16	5/28	6/12	—	8/28	—
Red Osier Dogwood	1971	—	4/27	4/27	5/19	5/11	7/8	5/26	6/9	6/18	8/25	9/30	9/30
	1972	—	4/28	5/6	5/27	5/12	7/25	6/2	6/13	6/20	8/1	9/26	9/26
	1973	4/15	4/23	4/23	5/28	5/9	7/23	5/28	6/4	6/12	7/23	10/2	10/2
Redstem	1971	—	4/27	5/4	5/26	5/11	7/8	5/19	6/2	6/9	7/27	—	10/8
	1972	4/19	5/6	5/12	6/2	5/19	8/12	5/27	6/13	6/13	8/1	—	—
	1973	4/3	4/23	5/2	6/4	5/16	6/26	5/16	6/4	6/4	8/3	—	—
Serviceberry	1971	—	5/4	5/4	5/19	5/11	7/8	5/11	5/19	5/26	8/25	9/23	9/23
	1972	—	5/6	5/12	5/27	5/19	6/13	5/19	5/27	6/2	7/25	9/26	10/9
	1973	4/15	5/2	5/11	5/28	5/16	6/12	5/9	5/28	6/4	7/23	—	—

TABLE 3. Continued

Snowberry	1971	—	—	4/21	5/4	4/27	5/26	6/18	6/30	6/30	9/23	10/8	9/30
	1972	—	—	4/19	5/12	4/28	6/13	6/13	6/27	6/27	8/31	—	10/9
	1973	—	4/3	4/15	5/9	4/15	6/4	6/12	7/4	7/12	8/28	—	—
Syringa	1971	—	—	4/21	5/11	5/4	5/26	6/24	6/30	7/14	—	9/23	9/23
	1972	—	—	4/19	5/27	5/6	6/13	6/20	7/3	7/3	—	9/26	9/26
	1973	—	4/5	4/15	6/4	5/7	6/27	6/19	7/4	7/12	—	10/2	10/2
Willow	1971	—	4/27	5/4	5/19	5/11	7/21	—	—	—	—	9/23	9/23
	1972	—	4/28	5/6	5/27	5/12	6/2	—	—	—	—	10/9	9/26
	1973	4/3	4/23	5/2	6/4	5/2	6/19	—	—	—	—	10/2	—

[1]The number preceding each / is the month; the number following each / is the day.

[2]End of bud swell refers to bud burst.

[3]End of fruit development refers to the time when fruits were mature (ripe).

—Indicates data were not collected.

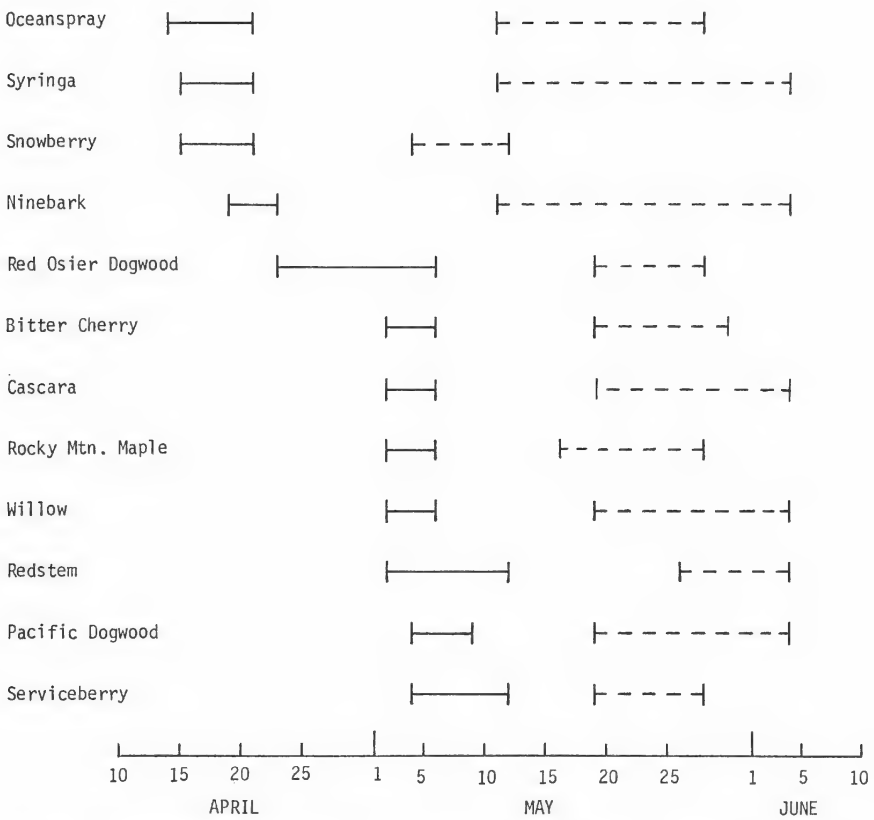

Figure 2. The range of dates for initiation (———) and completion (– – –) of leafing out.

ginning in mid-April for the three years. The remaining eight species—red osier dogwood, bitter cherry, cascara, Rocky Mountain maple, willow, redstem, Pacific dogwood, and serviceberry—generally initiated leaves during the first and second weeks of May.

The order for initiation of blooming among the 12 shrubs was constant and predictable (Fig. 3). Of the 12 shrubs studied, willow was the earliest to initiate flowering activity. Access to our study area was not possible during the time willow was blooming; therefore, no dates are available for this species.

Snowberry was always first to begin stem elongation as it occurred with leaf emergence. Bitter cherry was always the last shrub to begin stem elongation. In between snowberry and bitter cherry, the other ten shrubs varied their order of stem growth initiation (Fig. 4) from year to year.

Beginning of leaf color changes for eight of the twelve shrubs occurred generally between 23 September and 9 October (Table 3). Leaf color changes occurred earlier for Pacific dogwood and ninebark. Leaf color changes to yellow and brown were characteristic for six shrub species: bitter cherry, serviceberry, cascara, Rocky Mountain maple, willow, and syringa. Oceanspray, ninebark, and red osier dogwood leaves turned

orange and dull red, while Pacific dogwood leaves became a brilliant red. Snowberry and redstem leaves generally remained green.

Initiation of leaf fall generally coincided with the beginning of leaf color changes. Pacific dogwood was an exception; it was among the last shrubs to lose its leaves. Snowberry leaves began falling about 1 October even though they remained green. Redstem and cascara leaves were the last to start falling.

The completion of phenological events were not as predictable for year to year, and seldom was there a systematic order among the species. Species which initiated leaf emergence and stem elongation first were not necessarily the first plants to complete these activities (Figs. 2 and 4). An exception was snowberry since it was one of the earliest species to begin, and it was always the first plant to complete these

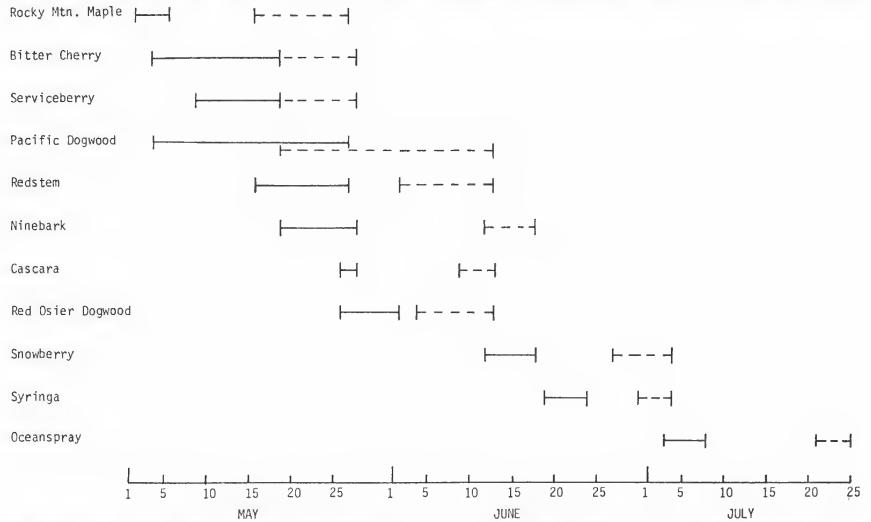

Figure 3. The range of dates for initiation (———) and completion (– – –) of blooming.

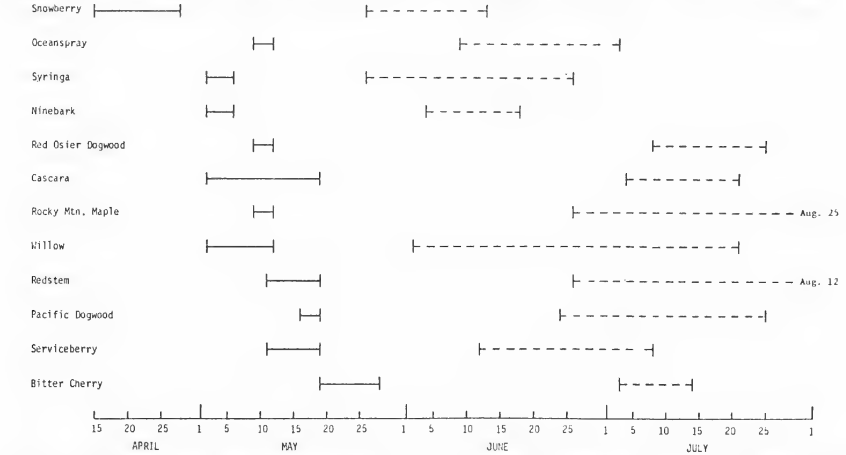

Figure 4. The range of dates for initiation (————) and completion (– – – –) of stem elongation.

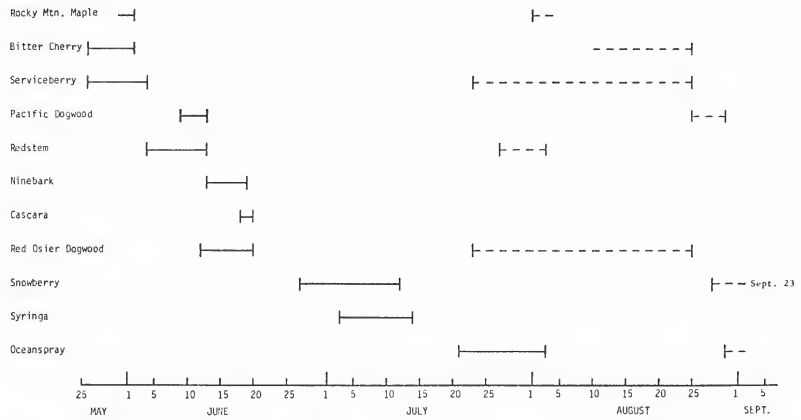

Figure 5. The range of dates for initiation (————) and completion (– – – –) of fruit development.

events. The order for completion of blooming among all of the species followed the order for initiation of blooming in almost all cases (Fig. 3). Completion of leaf color changes and end of leaf fall were not measured every year; therefore, it was not possible to correlate these events.

Beginning of fruit development coincided with the completion of blooming, and therefore occurred in predictable sequences (Fig. 5). However, the completion of fruit development varied greatly and followed no particular order from year to year.

Phenological Variations as Related to Weather

The date of initiation for each phenologic activity varied from year to year. Bud burst and stem elongation began earlier in 1973 for nine out of the 12 shrub species (Table 3). Two factors combined to promote the earlier activity in 1973. Maximum temperatures during March of 1972 and 1978 were significantly higher than in 1971 (Table 1) ($p = .05$). The last snow on the ground in 1973 was recorded on 18 February, whereas snow remained on the ground until 13 March in 1972 and 5 March in 1971. The fact that snow was gone by 18 February of 1973 might be the most important factor (Drew, 1967; Holway and Ward, 1965). Even though leaf emergence and stem elongation began earlier in 1973, blooming was not similarly affected.

Years of early initiation of stem elongation did not always coincide with years of longest duration for stem elongation. However, for nine of the 12 species, the year of greatest twig growth had the longest duration of stem elongation. Annual twig growth for redstem was significantly higher in 1972 ($p = .05$), while twig growth for the remaining 11 species was not significantly different among the three years. Annual twig growth for redstem has been correlated with the amount of precipitation during the period of May through August, with above average precipitation during July and August important for prolonging the growing period (Leege and Hickey, 1975). Precipitation for May-August for 1971-1973 was 21.2 cm, 19.1 cm, and 13.9 cm, respectively. However, the July and August precipitation was far above average in 1972, measuring 6.0 cm compared to 1.7 cm in 1971 and 0.6 cm in 1973.

Seed maturity (dissemination) was only documented accurately for eight species. For these, seed dissemination began earliest in 1973 for six species, in 1972 for one species, and for one species in 1971 (Table 2). The summer of 1973 was the driest of the three years, and this event could have had an effect on seed dissemination.

In 1971, leaf color changes occurred earliest for seven out of the 12 species, and leaf fall began earliest for eight of the 12 species. Early changes in leaf color usually resulted in early leaf fall.

Discussion

Plant phenology research has shown that many factors affect the starting of a plant's activities each year. Ahlgren (1957) found that dates of initial responses varied as much as a month from year to year, indicating that factors in addition to photoperiod and light intensity regulate seasonal development. Each phenological event also appears to be controlled by a different combination of factors.

Temperature and genetic factors are important agents regulating bud opening (McMillan, 1957; McMillan and Pagel, 1958; Morris *et al.*, 1957; Pauley and Perry, 1954). Snowmelt is an important factor affecting phenological activity of plants in spring (Drew, 1967; Holway and Ward, 1965).

Daylight hours from the last frost to the first leaf have been shown to be the most consistent parameter correlated with appearances of the first leaf. Soil temperatures and soil texture differences that influence water-holding capacity and subsequently temperature have also accounted for some plant response variation (Benacchio and Blair, 1972).

Initiation of twig growth has been correlated with air temperature (Halls and Alcaniz, 1972). Soil moisture is also a factor affecting the initiation of twig growth, depending upon the type of soil (Kozlowski, 1964).

Day length is an important factor controlling flowering in annuals (Went, 1953), while the wide variety in flowering times for some perennial species suggests the absence of a photoperiodic response (Holway and Ward, 1965; Lindsey and Newman, 1956). Jackson (1966) reported that earlier flowering species were most closely correlated with temperature while late flowering species were most closely correlated with photoperiod. Criddle (1927) and Moss (1960) found that early blooming plants (those which bloom by mid-May) have wider variations than late bloomers. Bingham and Squillace (1957) showed that early blooming pines are subject to the greatest variation in the timing of flowering. Genetic factors also have an effect on flowering (McMillan, 1957). Ahlgren (1957) suggests that flowering and leaf emergence follow bud swell within a given period of time.

Soil moisture affects the initiation of leaf color changes and leaf fall (Drew, 1967). Although in our study summer precipitation was lowest in 1973 with an extremely dry July and August (Table 1), leaf fall was earliest in 1971.

It appears that with so many different combinations of factors affecting phenological activities in plants, the calendar presented here is tenuous and subject to change. Drew (1967) studied the phenology of a young seral shrub community and provided an opportunity to compare initiation dates for some phenological events for eight of our 12 shrub species. His study sites were located approximately 144 km north of ours at 915 to 1037 m elevation in the Cedar/Hemlock zone. Drew was working with

five-year-old plants compared to plants about 35-40 years old in our study. He recorded two to four week earlier initiation dates for bud swell, leaf emergence, and stem elongation than we found. However, blooming initiation and initiation of fruit development fell within the ranges obtained in our study. Drew recorded the presence of snow on the ground on his sites as late as 25 March, while the latest snow on the ground on our study area was 13 March. Drew compared his records for bud break of serviceberry with unpublished records kept by the U.S. Forest Service. He noted that bud break was three to four weeks later in the Forest Service records and that the plants observed by the Forest Service were more mature plants.

We compared the sequence of phenological events for eight shrub species with findings from Drew (1967). For leaf emergence and blooming, the sequence of initiation was the same for his young plants as for our older plants, with the exception of serviceberry, which began leaf emergence earlier in sequence on Drew's sites. These were the two events found to be most consistent in sequence during our study. The consistency in sequence of flowering among species is well documented (Bingham and Squillace, 1957; McMillan, 1957).

Elevations, aspects, and position on slope will affect phenological activity because of their influences on variables such as temperature, snowmelt, soil moisture, and so forth. McLean (1972) reported the effect of elevation on shrub phenology in the Lochsa River drainage. Using several species of shrubs, he averaged the dates of initiation for six phenological events with the following results: for each 305 m increase in elevation between 457-1615 m, there was a time lag of nine days for bud break, nine days for full leaf emergence, nine days for stem elongation, ten days for full leaf, five days for flowering, and 16 days for fruit development. Personal observations indicate that vegetation in ravines and creek bottoms is usually slower to develop compared to higher slopes exposed to full insolation.

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Ectoparasites of the Virginia Opossum (Didelphis virginiana) in an Urban Environment

Abstract

Eleven species of fleas, mites, and ticks were collected from urban *Didelphis virginiana* during an 18-month study. Four species of mites and ticks represent new host records. Infestation is greatest during summer and fall.

Introduction

The Virginia opossum (*Didelphis virginiana* Kerr 1792) is a relatively recent arrival in Oregon. Many were brought to the state in the early 1930s by Civilian Conservation Corps (CCC) workers for food and/or pets; they escaped or were released by 1939 when the CCC was terminated (Mace, 1970). Known releases were made near Warrenton (Clatsop County) and Troutdale (Multnomah County). Opossums continued to expand their range, and on 24 March 1954 the Virginia opossum was first reported in northeast Portland where one was captured and taken to the Washington Park Zoo. In the ensuing 22 years, the opossum became abundant and ubiquitous throughout western Oregon.

Previous studies on the parasitology of opossums have been carried out in rural areas east of the Rocky Mountains. No studies have been reported concerning the animal's introduction in the western United States, nor its presence in urban areas. The purpose of this investigation was to study parasites that infest *D. virginiana* in a region occupied only recently by the species.

Methods and Materials

Seventy-seven opossums (excluding pouch young) were collected from December 1974 through May 1976, primarily from within the city limits of Portland (Multnomah County), Oregon. Eight opossums were from outside the city limits but within nearby urbanized areas. Except for two killed by dogs and one shot, all the animals were road kills.

The opossums were thoroughly combed and ectoparasites removed and preserved in 70 percent ethanol. Opossums were washed in 70 percent ethanol if large numbers of fleas were present to facilitate their capture.

Results and Discussion

Many ectoparasites, principally fleas, are known to infest opossums. At least 15 species

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of fleas are known to parasitize the animal (Potkay, 1970). In this study, the cat flea (*Ctenocephalides felis* Bouche), the dog flea (*C. canis* Curtis), and the Northern rat flea (*Nosopsyllus fasciatus* Bosc) were found. Both *C. felis* and *N. fasciatus* were common, neither occurring significantly more often than the other. *C. felis* has been the most commonly reported species in the past (Sandidge, 1953; Potkay, 1970). *N. fasciatus* has been reported only once previously, and then from just four opossums (Sandidge, 1953). *C. canis* has been previously reported on *D. virginiana* (Sanford and Hays, 1974). I found only one specimen of this flea.

Past studies have indicated that the opossum is relatively free of external parasites (Hamilton, 1958; Reynolds, 1945; Sandidge, 1953). This study, however, indicates the contrary, at least in Portland where infestation is frequent, although usually not severe. The higher rate of infestation may be attributable to the greater number of cats (*Felis catus*), dogs (*Canis familiaris*), and rats (*Rattus rattus* and *R. norvegicus*) found in an urban environment than in a rural one. The opossum likely exists in the same habitat as do rats and feral dogs and cats.

Frequency of flea infestation varied monthly, reaching a peak late in the year. Frequency during the winter was 53.3 percent; it increased slightly during the spring to 57.9 percent and in the summer to 66.7 percent. With the advent of fall, however, the frequency increased greatly to 92.3 percent.

Degree of infestation differs markedly between the sexes. Of 53 males examined, 38 (71.7 percent) were infested, but only 10 of 24 females (41.7 percent) were infested. The cause for this difference is unknown, but probably it is not due to a difference in grooming since there was no difference between sexes in the percentage of infested opossums with ingested fleas. No significant difference in the occurrence of fleas was found between juveniles and adults.

Nine species of Acari were removed from opossums; eight species of mites and one tick, in addition to 15 unidentified specimens, probably mostly nonparasitic. Five of the identified mite species are nonparasitic and are apparently accidentals; these include *Scheloribates* sp. (Orbatulidae), *Pergamasus* sp. (Parasitidae), *Ceratoppia* sp. (Metrioppidae), and *Poecilochirus necrophori* Vitzthum (Parasitidae). The other three are parasitic on mammals. All represented new host records, and all were taken from more than one animal. All are in the family Laelapidae; they are: *Androlaelaps fahrenholzi* (Berl.), *Haemogamasus nidi* (Michael), and *Eulaelaps stabularis* (Koch). Only one species of tick, *Ixodes angustus* (Neum.) was recovered. This, too, was a new host record.

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Characterization of Darkling Beetles Inhabiting Radioecology Study Areas at the Hanford Site in Southcentral Washington

Abstract

This two-year study was conducted to document the species composition and abundance of darkling beetles characteristic of biotic communities located near energy-related facilities at the Hanford Site in Southcentral Washington. A total of 7831 individuals representing 11 species were collected. The seasonal distributions of abundant species were compared between study years and between biotic community types.

Introduction

This paper reports on the kinds and abundance of darkling beetles inhabiting representative biotic communities on Department of Energy-owned lands comprising the Hanford Site near Richland in Southcentral Washington. Darkling beetles are a conspicuous component of northwest shrub-steppe communities, but little is known concerning their abundance, seasonal distribution, or species composition. Some important recent publications concerning the life histories and habits of northwest darkling beetles include Brown, 1973; Hinds and Rickard, 1973; Rickard, 1967; Rickard, 1970; Rickard and Haverfield, 1965; Rickard *et al.*, 1974; Rogers and Rickard, 1975; and Rogers *et al.*, 1978.

This study was conducted as part of an overall program designed to characterize the biota inhabiting areas near energy-related facilities. Four areas were selected for intensive study. Two were located near the Washington Public Power Supply System's nuclear power plant sites numbers 1 and 4 in mixed bitterbrush-sagebrush (*Purshia tridentata* (Pursh) DC. and *Artemisia tridentata* Nutt.) and bitterbrush communities, respectively. The bitterbrush community has an understory comprised of cheatgrass (*Bromus tectorum* L.) and bluegrass (*Poa sandbergii* Vasey). The bitterbrush-sagebrush community has an understory of cheatgrass with only a trace of bluegrass present.

The two other study areas chosen were sagebrush-dominated communities with cheatgrass understories. One of these was located near a low-level radioactive waste burial site known administratively as the B-C cribs and managed by the Rockwell Hanford Operations Company. The other study area was located on the nearby Arid Land Ecology (ALE) Reserve. The ALE Reserve encompasses an approximate 120 mi^2 area along the eastern slope of the Rattlesnake Hills that has been set aside for ecological studies of semi-arid shrub-steppe communities in the Northwest. The study plot on the ALE Reserve, protected from disturbance, is intended to serve as a control

for those study areas located near the nuclear power plants and radioactive waste storage areas.

Methods

The beetles were sampled within each of the study areas by pitfall trapping. The traps consisted of twenty-five 15 cm x 15 cm metal cans buried flush with the rims. A 30 cm x 30 cm board was placed over the opening of each trap to serve as a rain guard. The traps were set out in a grid system at 5-m intervals in April 1976 and checked at weekly intervals through November when they were closed for the winter. They were opened again in March of the following year and checked through 4 October 1977. Captured beetles were removed by hand, tabulated, and released near their point of capture.

Results and Discussion

The seasonal pattern of total darkling beetle abundance for each of the study areas is shown in Figure 1. Although there are differences in total beetle numbers for

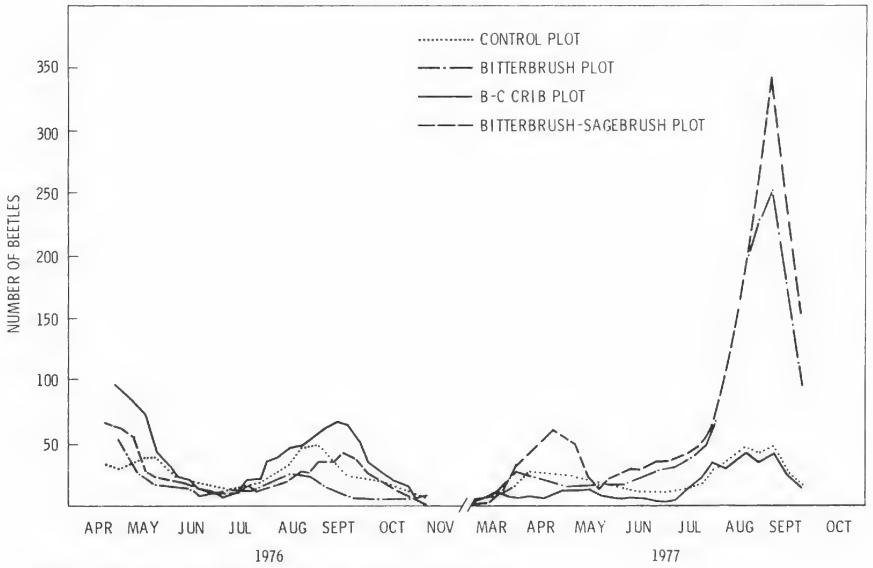

Figure 1. Seasonal pattern of darkling beetle abundance.

particular sample dates, the same general trends appear to have occurred in all study areas during 1976. Similar trends continued during the early 1977 season, but by June, substantially greater catches occurred in the bitterbrush and bitterbrush-sagebrush plots. The catches in the control and B-C crib plots remained equivalent throughout 1977. These kinds of periodic fluctuations appear to be characteristic of darkling beetles, although the reasons remain unclear (Brown, 1973).

The total number of individuals of each species captured during the two study years is shown in Table 1. A total of 7831 individuals representing 11 different species

TABLE 1. Darkling beetle abundance during 1976 and 1977 study years.

Species	Control		B-C Crib		Bitterbrush		Bitterbrush-Sagebrush	
	1976	1977	1976	1977	1976	1977	1976	1977
Eleodes hispilabris Say	404	278	344	219	193	280	358	429
Eleodes novoverrucula Bod.	153	40	90	38	191	166	198	178
Eleodes humeralis LeC.	56	93	81	83	56	62	10	29
Eleodes nigrina LeC.	55	47	5	6	5	11	5	29
Eleodes granulata LeC.	18	4	12	10	10	2	14	1
Eleodes obscura Say	0	1	0	0	24	24	0	5
Eusattus muricatus LeC.	20	38	310	3	5	54	0	18
Coniontis setosa Csy.	55	35	131	16	17	959	41	1323
Conisattus nelsoni Bod.	0	0	0	0	0	3	0	0
Oxygonodera hispidula Horn	0	0	0	0	0	1	0	0
Philolithus densicollis (Horn)	37	21	180	39	1	0	135	72
TOTAL	798	557	1153	414	502	1562	761	2084

were collected. Six species accounted for over 90 percent of the total beetle catch. These included *Eleodes hispilabris* Say, *E. novoverrucula* Bod., *E. humeralis* LeC., *Eusattus muricatus* LeC., *Coniontis setosa* Csy., and *Philolithus densicollis* (Horn). The seasonal distribution of these species is shown in Figure 2. *E. hispilabris* was

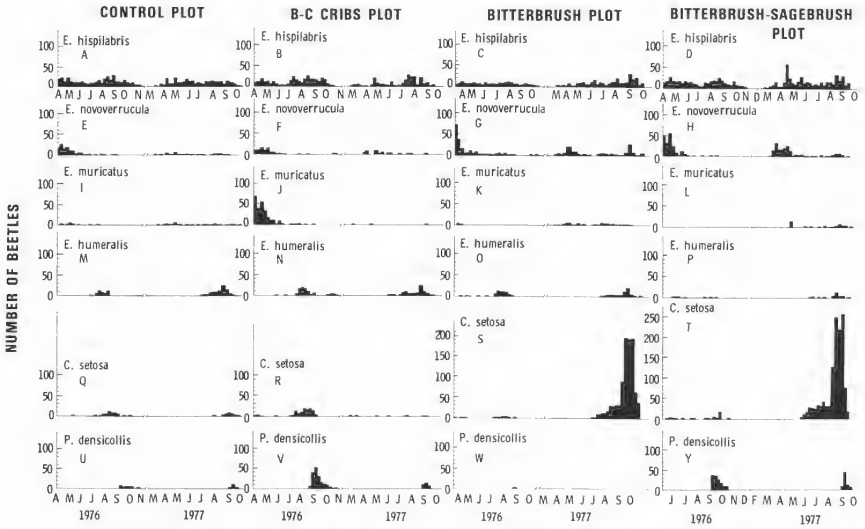

Figure 2. Number of beetles captured each week within each study area.

consistently captured during all study periods without a discernible seasonal peak in abundance (Fig. 2A-D). All other species shown in Figure 2 appear to be particularly abundant during some portion of the season. *E. novoverrucula* (Fig. 2E-H) and *Eusattus muricatus* (Fig. 2I-L) were most abundant during the months of April and May; *E. humeralis* numbers peaked during the July and August months (Fig. 2M-P). *C. setosa* abundance peaked during August and September. *C. setosa* is a widely distributed species on Hanford lands (Rogers *et al.*, 1978) but was not previously known to occur at the levels detected in the bitterbrush and bitterbrush-sage-

brush plots during 1977 (Fig. 2Q-T). *P. densicollis* is a fall emergent species and only occurred during the months of September and October (Fig. 2U-Y).

The five remaining species, *Eleodes nigrina* LeC., *Eleodes granulata* LeC., *Eleodes obscura* Say, *Conisattus nelsoni* Bod., and *Oxygonodera hispidula* Horn, occurred at population levels too low to permit discernment of possible peaks of seasonal abundance. Both *Eleodes nigrina* and *Eleodes obscura* are common darkling beetles at Hanford but are never particularly abundant (Rogers *et al.*, 1978). *E. granulata* occurred in low numbers in all plots during this study (Table 1). This result is supported by a previous study (Rogers *et al.*, 1978) in which *E. granulata* was found to occur primarily in sagebrush/bunch grass (*Artemisia tridentata* Nutt./*Agropyron spicatum* (Pursh) Scribn. and Smith) and winterfat (*Eurotia lanata* (Pursh) Moq.) communities, with only infrequent sightings at other locations.

Conisattus nelsoni and *O. hispidula* are regarded as rare and not common species, respectively (Hatch, 1965). However, they may be locally abundant on occasion at Hanford (Rogers *et al.*, 1978). Both species were extremely rare during this study with only one *O. hispidula* and three *C. nelsoni* captures made during the entire two years. (Table 1).

Summary

This characterization of darkling beetle populations inhabiting biotic communities located near energy-related facilities is intended to provide baseline values for future evaluations.

Six species comprised most of the trap catch. *Eleodes hispilabris* was consistently captured at high levels in all study areas and at all times. *Eusattus muricatus, Eleodes novoverrucula, E. humeralis, C. setosa*, and *P. densicollis* were abundant during certain seasonal periods within specific study areas.

Acknowledgments

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Quantitative Analysis of Pika (Ochotona princeps) Hay Piles in Central Idaho

Abstract

Eleven hay piles of a pika (*Ochotona princeps*) colony in central Idaho were quantitatively examined. Twenty-six plant species were identified: *Smilacina stellata, Apocynum androsaemifolium,* and *Fragaria virginiana* comprised 88 percent of the total weight of all hay piles.

Introduction

The pika (*Ochotona princeps*) is a common inhabitant of talus slopes in the mountains of western North America (Cahalane, 1947). A characteristic habit of this mammal is the construction of hay piles to serve as a source of food in winter (Millar and Zwickel, 1972). Many authors have reported gross qualitative examinations of hay piles (Rausch, 1962; Johnson, 1967; Bates, 1969; Bunnell, 1970), but few quantitative examinations have been reported (Beidleman and Weber, 1958; Millar and Zwickel, 1972). The purpose of this study was to examine quantitatively the hay piles of a pika colony in central Idaho.

Study Area and Methods

During the summer (May-August) of 1978, hay piles of a pika colony on the west slope of Hogback Ridge (elev. 1862 m), Payette National Forest, Valley County, Idaho, were examined. Individual hay piles were located and marked; plant species and stored material in each pile were identified, and in August all material was individually weighed to the nearest gram. The distance between hay piles and the distance of each pile from the edge of the talus was measured.

Results

Eleven hay piles were located and examined. Twenty-six plant species were identified (Table 1). *Smilacina stellata* (Starry solomonplume), *Apocynum androsaemifolium* (spreading dogbane), and *Fragaria virginiana* (strawberry) were the most frequently encountered plant species in hay piles, and comprised 88 percent of the total weight of all hay piles.

Discussion

Millar and Zwickel (1972) reported that small hay piles of pikas in Alberta were located between or under the edge of rocks—the larger piles were found under fallen trees and showed evidence of being placed on top of previous season's hay piles. This vegetation storage site preference was also exhibited by the Hogback Ridge colony. Small hay piles were found in the talus while those piles in excess of 300g (n=2)

were found on top of old hay piles under fallen trees. Observations of other down trees in the area revealed large caches of previous season's hay piles; no such large accumulations of new or old vegetation were observed in the talus.

TABLE 1. Items identified in hay piles of pika from central Idaho, 1978.

Item	Amt. Present	% Total Wgt.	% Freq.
Smilacina stellata	575g	70.5	100
Apocynum androsaemifolium	90	11.0	63
Fragaria virginiana	51	6.3	81
Marmot scat	48	5.8	18
Angelica arguta	10	1.2	9
Vaccinium scoparium	8	0.9	18
Calamagrostis rubescens	8	0.9	18
Senecio pauciflorus	5	0.5	9
Erigeron speciosus	4	0.4	36
Rubus idaeus	4	0.4	18
Agropyron caninum	3	0.3	36
Carex microptera	3	0.3	18
Potentilla fruticosa	2	0.2	54
Achillea millefolium	2	0.2	45
Poa pratensis	2	0.1	9
Sedum stenopetalum	1	0.1	18
Cirsium utahense	1	0.1	9
Equisetum arvense	1	0.1	9
Astragalus alpinus	1	0.1	9
Arnica longifolia	1	0.1	9
Antennaria microphylla	1	0.1	9
Bromus tectorum	1	0.1	9
Galium aparine	1	0.1	9
Trifolium spp.	1	0.1	9
Epilobium angustifolium	1	0.1	9
Frasera speciosa	1	0.1	9
Gaultheria humifusa	1	0.1	9
TOTAL	827	100.0	

Plant nomenclature according to Hitchcock and Cronquist (1973).

Broadbooks (1965) reported pikas in Washington prefer the borders of talus slides rather than the middle, and found that the average distance between hay piles on main slopes was 70 m. All main hay caches Broadbooks (1965) examined were within 9 m of the lower edge of the talus slope. The Hogback Ridge colony placed their stores within an average of 4.5 m of the meadow's edge and averaged 0.7 m between hay piles.

Marmot (*Marmota flaviventris*) scats were found in the larger hay piles (Table 1). Broadbooks (1965) observed "dozens" of marmot scat associated with hay piles and concluded that they had been deliberately stored for the winter. Pikas reingest their own fecal material (Haga, 1960), these pellets having been found to have high energy and protein values (Johnson, 1967). Marmot scats may thus be utilized as an auxillary source of protein in those areas coinhabited by pikas and marmots.

Total weights of hay piles in late August were extremely variable, ranging from about 5 g to over 300 g. Broadbooks (1965) noted that a large amount of hay material could be accumulated by pikas in a short time. Barash (1973) observed that there is a significant late seasonal increase in the frequency of haying trips; thus, it is possible that the number and total weight of hay piles on Hogback Ridge could have increased after the sampling period.

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Fleas (Siphonaptera) from Nests and Burrows of the Bank Swallow (Riparia riparia) in Alaska

Abstract

Fleas collected from 36 vacated nests and 18 active and inactive burrows of the Bank Swallow in Alaska south of the Yukon River and west of the Yukon Territory totaled 1503 (57 percent females) *Ceratophyllus styx riparius* Jordan and Rothschild and 62 (66 percent females) *C. c. celsus* Jordan. The two taxa were collected from 19 and 9 localities, respectively. *C. c. celsus* outnumbered *C. s. riparius* only at the southernmost locality. The ranges of *C. styx riparius* and *C. c. celsus* were extended 465 and 700 km southwestward, respectively. Females of both taxa have a rather variable posterior margin of sternum VII.

Introduction

This report is the second concerning our survey of ectoparasites of swallows in Alaska. In concurrence with results of the only other study of fleas of Bank Swallow (*Riparia riparia* (Linnaeus)) nests and burrows in Alaska (Hopla, 1965), we collected large numbers of *Ceratophyllus styx riparius* Jordan and Rothschild and small numbers of *Ceratophyllus celsus celsus* Jordan. We extended the ranges of *C. styx riparius* 465 km and *C. c. celsus* 700 km from southcentral Alaska southwest to the Alaska Peninsula, the only locality where *C. c. celsus* outnumbered *C. s. riparius.* Females of both taxa have a rather variable posterior margin of sternum VII.

Procedures

Bank swallow nest sites were sought south of the Yukon River and west of the Yukon Territory from 1973 to 1978. Vacated nests were removed from burrows with a trench shovel and longhandled forceps during April-May and July-October. Nests from the same colony were pooled in one bag, carried to the laboratory, and carefully broken apart in a pan. Fleas were captured with a light-weight forceps. Selected individuals were cleared and permanently mounted in Canada balsam, others were preserved in 70 percent ethanol, and all were identified, sexed, counted, and labelled. Specimens were deposited in the Agriculture Canada Biosystematics Research Institute, Ottawa, and in the authors' collections.

Supplementary collections of fleas were made from burrow entrances, particularly

in June when birds were nesting. Fleas that aggregated at burrow entrances were captured using forceps, a piece of white flannel cloth, and a dish pan. Some fleas were so stimulated by shadows and breath of the collectors that they jumped or crawled out of burrows and were captured from some projection below.

Infested nests and burrows were pooled separately except at collection locality I (see list below), where they were pooled together (Table 1). Uninfested burrows and nests were observed in most colonies but were not routinely counted and recorded as occupancy histories were unknown.

For brevity in presentation of results (Table 1), collection localities were alphabetically assigned the following code letters:

A. Anchorage, 30 km SE: mound between Seward Hwy and Turnagain Arm;
B. Brushkana Cr., 4.8 km W: road cut along Denali Hwy;
C. Cohoe, 8 km S: gravel pit along Cohoe Rd;
D. Eagle: bluff along Yukon R;
E. Ernestine: gravel pit along Richardson Hwy;
F. Fairbanks, 48 km WSW: road cut along Parks Hwy;
G. Houston: gravel pit near Parks Hwy;
H. Kasilof, 1.6 km S: road cut along Sterling Hwy;
I. King Salmon, 9.3 km SE: bluff on point in bend of Naknek R;
J. Knik, 1.6 km N: gravel pit near Knik Rd;
K. Lower Tonsina, 0.5 km N: road cut along Edgerton Hwy;
L. Palmer, 7.1 km W: road cut along Bogard Rd;
M. Palmer, 9.6 km N: road cut along Buffalo Mine Rd;
N. Paxson, 1.6 km N: gravel pit along Richardson Hwy;
O. Soldotna, 16.4 km E: road cut along Sterling Hwy;
P. Soldotna, 29 km E: road cut along Sterling Hwy;

TABLE 1. Fleas (**Ceratophyllus**) from Bank Swallow nests and burrows in Alaska, 1973-1978.

Nest (Burrow) Number	Locality	Date	C. styx riparius ♂♂	C. styx riparius ♀♀ sternum VII narrow	C. styx riparius ♀♀ ventral lobe broad	C. styx riparius Total	C. c. celsus ♂♂	C. c. celsus ♀♀	C. c. celsus Total
(1-4)	M	16.IX.73	12	14	0	26	0	0	0
(6-9)	M	20.VI.74	3	10	0	13	0	1	1
1-3	G	21.IV.74	42	27	2	71	0	0	0
5	G	26.VII.74	0	1	0	1	0	0	0
6-8	G	31.VII.74	1	4	3	8	0	0	0
4	K	25.V.74	4	18	0	22	1	2	3
13-15	K	10.VIII.74	27	42	0	69	0	4	4
(5)	H	10.VI.74	1	4	0	5	1	3	4
(10-15)	A	22.VI.74	30	62	5	97	1	7	8
9-10	R	31.VII.74	6	2	1	9	0	0	0
11-12	E	10.VIII.74	5	9	0	14	0	0	0
16	N	17.VIII.74	40	22	0	62	1	3	4
17-19	B	18.VIII.74	1	2	0	3	0	0	0
20*	Q	19.VIII.74	18	36	0	54	0	0	0
21	J	23.VIII.74	80	96	5	181	3	2	5
22-25*	F	6.IX.74	76**	87	0	163	6	9	15
26	L	12.IX.74	264	304	15***	583	0	0	0
27	P	14.IX.74	5	3	1	9	1	0	1
28*	O	do	5	11	7	23	0	0	0
29	C	15.IX.74	8	7	0	15	0	0	0
30-31	D	11.VIII.75	5	37	0	42	0	0	0
32-34 + (16-18)	I	4.X.77	2	2	0	4	7	10	17
35-36	S	31.VIII.78	15	14	0	29	0	0	0
TOTALS			650	814	39	1,503	21	41	62

*Only sample of fleas collected.
**Includes 1 intersex (see Haas, 1980).
***Includes 1 intergrade.

Q. Wasilla, 4 km S: gravel pit along Fairview Lp;
R. Willow: gravel pit near Hatcher Pass Rd; and
S. Yukon R. Bridge of Yukon-Prudhoe Hwy, 1.6 km E: road cut along Hwy.

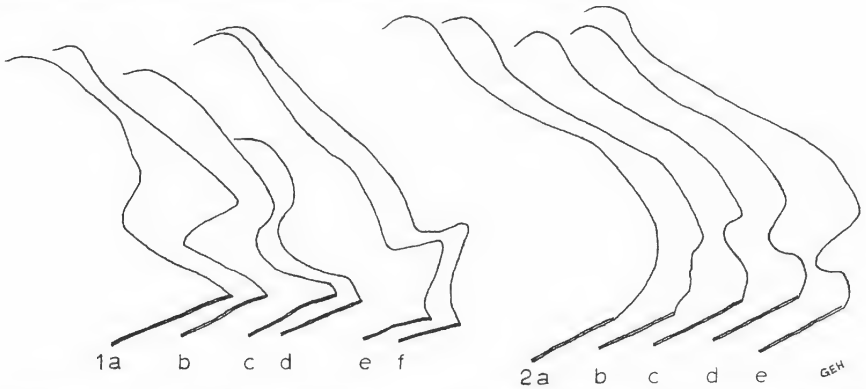
Collection data are presented in Table 1 chronologically.

Results

Two taxa were collected: *Ceratophyllus styx riparius* Jordan and Rothschild and *C. celsus celsus* Jordan (Table 1). The first occurred in all 19 localities surveyed, predominated in 18 of them, and represented over 96 percent of the total collection with 1503 specimens. The second occurred in nine localities, predominated in one, and represented less than 4 percent of the total collection with 62 specimens.

Collections near King Salmon, Alaska Peninsula (locality I), extended the range of *C. styx riparius* 465 km southwest from Potter, Turnagain Arm (Hopla, 1965), and the range of *C. c. celsus* 700 km southwest from the Susitna River, Denali Highway (Haas and Wilson, 1980).

Table 1 lists counts of *C. styx riparius* females by 2 sternum VII morphological types. One of the 39 specimens tabulated under broad ventral lobe actually is an intergrade (Fig. 1 c & d). Therefore, 38 of 853 females (4.4 percent) are truly in the broad lobe group. Morphological variations in *C. c. celsus* females were not tabulated. The shape of the posterior margin of sternum VII intergrades from a single well-rounded lateral lobe to a moderately deep lateral sinus (Fig. 2 a-e).



Figures 1 and 2. Variations in outline of sternum VII of females of (1) *Ceratophyllus styx riparius* Jordan and Rothschild (a from locality M, b from loc R, c and d left and respective right side of specimen from loc L, e and f from loc L); (2) *Ceratophyllus celsus celsus* Jordan (a from loc A, b from loc F, c and d from loc J, e from loc K).

Discussion

Riparia riparia, the Bank Swallow, breeds widely in the Northern Hemisphere and winters in South America, Africa, and southern Asia (Peterson, 1961). Gabrielson and Lincoln (1959) and Kessel and Gibson (1978) described this colonial swallow as a common and locally abundant breeder throughout central Alaska from mid-to late May to mid-August, and indicated that there are peripheral breeding records for western, southwestern, the north Gulf Coast-Prince William Sound region, and southeastern Alaska. The birds winter in South America.

Breeding habits of these swallows are especially favorable for high infestation of nests by arthropods. Burrowing and nesting are described by Gabrielson and Lincoln (1959) and Harrison (1975). Colonial habits; long, narrow burrows in the earth; nests of organic matter; and reuse of burrows in successive years are ecological factors favorable for nest-fleas. Many studies of fleas in *R. riparia* nests in Europe, Asia, and North America have been published (see Hicks, 1959, 1962, 1971). Several species of bird fleas and even mammal fleas were recorded, but the only true *R. riparia* nest-fleas are *Ceratophyllus styx* Rothschild, *C. celsus celsus* Jordan, and *Frontopsylla lapponica* (Nordberg). They are Holarctic, Nearctic, and Palaearctic, respectively.

Ceratophyllus styx has four recognized subspecies: *C. s. styx* ranges through most of the European Subregion of the Palaearctic Region and Kasakhstan, and *C. s. jordani* Smit ranges through the British Isles except in areas in the south, southeast and east of England where it is replaced by the nominate subspecies (Smit, 1955; Rothschild and Smit, 1955; Smit, 1969). *Ceratophyllus s. freyi* Nordberg replaces *C. s styx* in northern Scandinavia and Finland (Smit, 1969; Brinck-Lindroth and Smit, 1971). *Ceratophyllus styx riparius* Jordan and Rothschild ranges from Trans-Baykalia, Mongolia, and Japan to North America (Smit, 1967; Lewis, 1975; Ono, 1964).

Ceratophyllus c. celsus has a broad transcontinental range in North America occurring in nests of Bank Swallows and Cliff Swallows (*Petrochelidon pyrrhonota* (Vieillot)) depending on geographic location (Benton and Shatrau, 1965; Hicks, *loc. cit.*; Nelson, 1972). *Frontopsylla lapponica* is known from northern Sweden and Finland and also from Trans-Baykalia and Mongolia (Smit, 1967; Brinck-Lindroth and Smit, 1971).

The first study of fleas in nests and burrows of Bank Swallows in Alaska was by Hopla (1965), who reported on one small collection (1 male, 1 female *C. s. riparius*) at Potter, Turnagain Arm, and on many large collections in central Alaska. His total collections were 13,940 *C. s. riparius* from 80 nests and 47 *C. c. celsus* from seven nests. One *C. idius* Jordan and Rothschild, usually found in nests of Tree Swallows (*Iridoprocne bicolor* (Vieillot)), and two *C. scopulorum* Holland, a nest-flea of the Cliff Swallow, were also found.

We found only *C. s. riparius* and *C. c. celsus* in nests and burrows of Bank Swallows, and as usual for bird fleas (Rothschild, 1952), females predominated in both taxa. The 1503 *C. s. riparius* recorded in Table 1 consisted of 56.8 percent females. This figure is rather close to 55.9 percent calculated from Hopla's (1965) data (7800 females). In contrast, his *C. c. celsus* data were remarkably close to equality (23 males and 24 females; i.e., 51 percent females). Our larger collection of 62 individuals (Table 1) consisted of 66 percent females, and when data from both studies were combined (44 males, 65 females), females were still highly predominant at 60 percent. This figure suggests that, with an exception discussed below, conditions in Bank Swallow nests and burrows in Alaska are not as favorable for this taxon as for *C. s. riparius*. Less than 4 percent of our total collection was *C. c. celsus*; only 0.003 percent of Hopla's (1965) collection was *C. c.* celsus.

While extending ranges of *C. s. riparius* and *C. c. celsus* southwestward, we detected a trend for the second taxon to increase in number relative to the first. Hopla (1965) anticipated this sort of shift when he wrote that it would be interesting to see if *C. c. celsus* is prominent in Bank Swallow nests in southeastern Alaska. From data in

Table 1, it can be calculated that if fleas from only single and pooled nests infested with *C. c. celsus* are totaled, this taxon increases from less than 4 percent to 6 percent (32 of 537 fleas). As these localities were widely scattered, a southward weighting is necessary. Thus, if the same calculations are applied to burrow collections near Cook Inlet in June, when no nests were collected, we note *C. c. celsus* increases to 10 percent (13 of 128 fleas). If all burrow collections including the burrow and nest pool near King Salmon (locality I) are used in the calculations, *C. c. celsus* increases to 17 percent (30 of 175 fleas). Furthermore, as shown in Table 1, *C. c. celsus* predominated at locality I with 17 of 21 fleas (80 percent).

Females of both *C. s. riparius* and *C. c. celsus* have a rather variable posterior margin of sternum VII. The first taxon is almost dimorphic, there being but a single intergrade (tabulated under broad lobe) (Fig. 1 c & d). Most specimens are of the usual type, i.e., with a narrow ventral lobe below a deep sinus (Fig. 1 a & b), but 38 specimens from seven localities near Cook Inlet (Table 1) have a broad ventral lobe without the sinus above (Fig. 1 e & f). This form was reported from New Brunswick and illustrated by Benton and Shatrau (1962; Fig. 1). They reported this dimorphism (there were no intergrades) occurred in 15.5 percent of 135 specimens. We recorded 5.8 percent (38 of 658) of *C. s. riparius* collected from localities near Cook Inlet with the broad lobe. Broad-lobed specimens of *C. s. riparius* are known also from Japan. Ono (1964) reported 73 (12.4 percent) of 590 females from Hokkaido with the same form of lobe as certain specimens of *C. s. freyi* in Finland (cf. Fig. 3 g & h, Ono; Fig. 16 c-g, Smit, 1956). Smit (1955) noted in his description of *C. s. jordani* that a population from one locality in Britain had a wide range of variation from the broad ventral lobe to the narrow *C. r. riparius* (=*C. s. riparius*) type. Our intergrade (Fig. 1 c & d) from near Palmer (locality L) falls within the range of variation as illustrated in his Fig. 79. We cannot explain why the broad-lobed form of *C. s. riparius* appeared in our collections only from near Cook Inlet, but its presence in Alaska strengthens the concept of a Holarctic *C. styx*.

The posterior margin of sternum VII of *C. c. celsus* varies continuously from a single, well-rounded lateral lobe to a lateral sinus (Fig. 2). In three specimens the sinus is shallow (e.g., Fig. 2 c). In two other specimens, the lateral sinus is deeper (Fig. 2 d & e). Keys to North American bird fleas in the genus *Ceratophyllus* should indicates that *C. s. celsus* females, as well as those of *C. niger* Fox and *C. petrochelidoni* Wagner (see Holland, 1951), may have a sinus in the posterior margin of sternum VII.

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Cheatgrass Communities: Effect of Plowing on Species Composition and Productivity

Abstract

Thirty-year-old cheatgrass communities were disturbed by experimentally plowing small plots. Cheatgrass, *Bromus tectorum* L., promptly invaded the plowed plots. Plowing enhanced plant production at the high elevation site, 520 m, but depressed production at the low elevation site, 320 m, during a year of near normal precipitation in 1976. During the 1977 drought, plant production was very low at both study sites, but productivity was most depressed at the low elevation site. Possible factors in the explanation of results are discussed.

Introduction

Lands that support natural plant communities in the shrub-steppe region of south-central Washington have steadily diminished over the years as dryland and irrigated agricultural practices have steadily expanded, encroaching upon native plant communities. Once under cultivation the land is usually retained under crop management and not permitted to undergo a self-revegetation process. Daubenmire (1975) reports that an abandoned cultivated field in southeastern Washington was dominated by cheatgrass, *Bromus tectorum* L., for 50 years with little or no invasion by native grasses and shrubs. There apparently is no quantitative information to judge what to expect if old, stable cheatgrass communities are disturbed by plowing and allowed to be self-revegetated.

Two agricultural fields on the U.S. Department of Energy's Hanford Site have been abandoned since 1943 and have not since been disturbed. These fields have been dominated by cheatgrass for three decades. The fields are within 5 km of each other. One field is located at an elevation of 305 m above sea level and the other at 520 m. These fields have been previously described by Cline and Rickard (1973). The low elevation field is small, about 10 ha; but the high elevation field is several hundred ha in extent.

Four small plots, each 10 x 20 m, were plowed on each field in late autumn 1974 as a way to initiate bare ground plant colonization. Both fields were sampled for above-ground productivity and species composition by comparison with adjacent unplowed (control) ground. Harvests were made in the spring of 1976 and 1977, and the results are presented in this report.

Methods

Harvests of live phytomass were made three times during the spring of 1976 and

1977; early, middle, and late in the growing season. Small circular plots, 0.032 m^2, were hand harvested and the live material segregated by species. At each harvest period, five points were randomly selected within each treatment. Dead plant material, standing and prostrate and termed "mulch," was also harvested. Mulch was removed by hand until mineral soil was visible. Care was taken to avoid incorporating mineral soil into the mulch sample. All harvested material was oven dried at temperatures between 50-60°C and weighed. A one-way analysis of variance was performed to test the statistical validity of the harvest estimates (Table 1).

A rain gauge was maintained at each field and read each month. The October to May precipitation was of most concern since this period represents the growth season for cheatgrass and its associated annuals.

TABLE 1. Analysis of variance of phytomass on control and plowed plots, May 21, 1976.[1]

	Location	Treatment	n	$\bar{x}$	SD	CV	ANOVA
Live Phytomass	Upper Field	Plowed	20	9.68	4.7	0.49	$P(F)=0.00011$
		Control	10	2.73	1.3	0.49	
	Lower Field	Plowed	20	5.28	0.23	0.06	$P(F)=3.8 \times 10^{-7}$
		Control	10	9.42	1.9	0.21	
Dead Phytomass (Mulch)	Upper Field	Plowed	20	1.27	1.9	1.47	$P(F)=8.2 \times 10^{-9}$
		Control	10	12.6	5.8	0.46	
	Lower Field	Plowed	20	1.40	1.5	1.06	$P(F)=0.00$
		Control	10	11.5	1.7	0.15	

[1]Mean based on 0.032 m^2 plots.

Results and Discussion

Harvests were not made during the spring of 1975 because of the lateness of the plowing in 1974. Harvest results in 1976 and 1977 are shown in Figures 1 and 2. The 1977 growing season was marked by extreme drought: only 6 cm of precipitation was recorded in the low elevation field and only 8 cm on the high elevation field during the period October to May. In 1976, the October through May precipitation amounted to 17.0 cm in the low field and 18.9 cm in the high field. In 1976, production on the unplowed (control) plots at the high elevation was relatively low, only 87 g/m^2 (Fig. 1) in relation to the amount of precipitation. This fact was surprising because in 1977 production was 83 g/m^2 and the precipitation was only one-third that of 1976. The plowed plots in 1976 were almost three times more productive than control plots 240 g/m^2 as compared to 87 g/m^2. In 1977, the plowed plots yielded 35 g/m^2 and control plots 83 g/m^2; the difference suggests that the high yield on the plowed plots in 1976 depleted the soil in some way that was important to plant growth. Rickard and Cline (1975) hypothesize that nitrogen may be the factor limiting growth on the upper field rather than the scarcity of rainfall.

At the low elevation field, the control plots were more productive than the plowed plots, 292 g/m^2 as compared to 164 g/m^2 in 1976 (Fig. 1). In 1977 productivity was extremely low in both control and plowed plots; and it is attributed to the extreme drought.

The nearest ecological counterpart to the cheatgrass community is California's

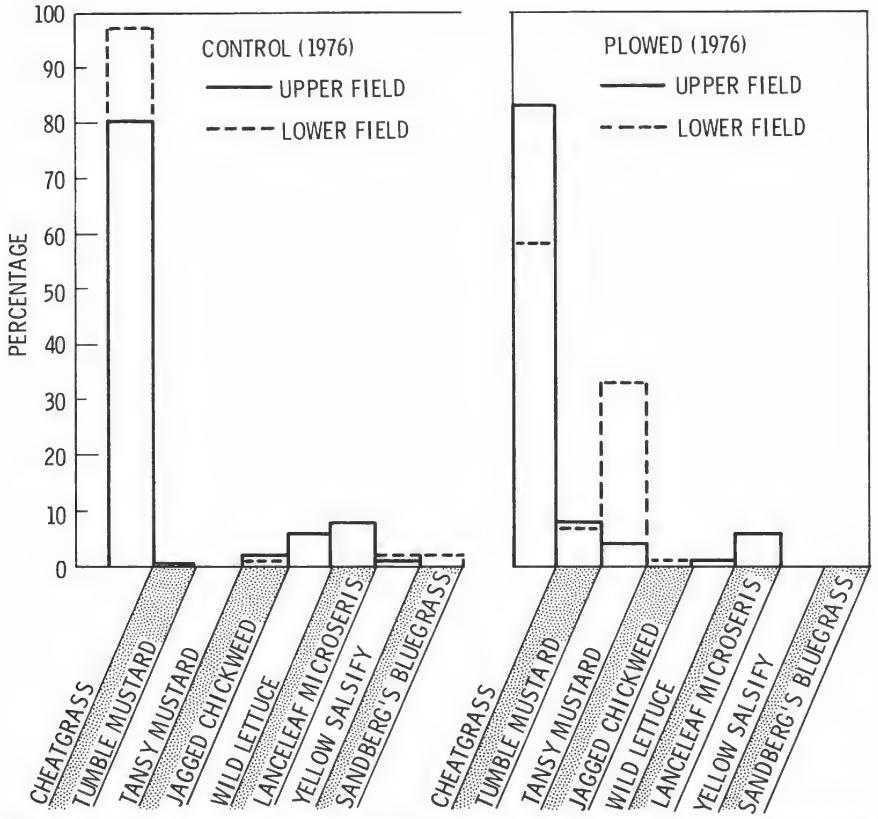

Figure 1. Live aboveground phytomass harvested from control and plowed plots during the spring of 1976 and 1977 at the upper and lower fields.

annual grassland. Mulch is regarded as an important feature of the California annual grassland community. Mulch removed prior to the seed germination period greatly reduced plant production (Hooper and Heady, 1970). Changes in botanical composition were also related to mulch accumulation (Heady, 1958, 1961). In our study, plowing effectively removed most of the mulch from the surface and placed it below the surface. Clearly the plowed plots in 1976 did not have as much mulch as the control plots (Fig. 2). Mulch removal by plowing enhanced plant production in the upper field in 1976 but depressed production on the lower field (Fig. 1). Enhanced production in 1976 contributed to the enhanced mulch accumulation on the plowed plots at the upper field in 1977, indicating that decomposition of dead plants is not very rapid.

The cheatgrass community is characterized by low species diversity (Fig. 3). After 30 years, most of the species are alien annuals. Only one native grass species was recorded on the study plots, sandberg bluegrass, *Poa sandbergii* Vasey. Lance leaf microseris, *Microseris lanciniata* (Hook). Schultz-Bip., a perennial forb and yellow salsify, *Tragopogon dubius* Scop., a biennial forb, were found only on the upper field.

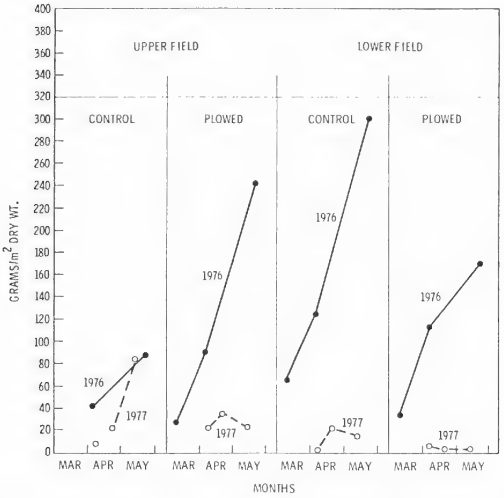

Figure 2. Dead aboveground phytomass (mulch) harvested from control and plowed plots during the spring of 1976 and 1977 at the upper and lower fields.

Cheatgrass, *Bromus tectorum* L., Tansy mustard, *Descurainia pinnata* (Walt.) Britt., jagged chickweed, *Holosteum umbellatum* L., and wild lettuce, *Lactuca serriola* L., were also present. In 1976 control plots were predominantly cheatgrass, but the plowed plots on the lower field supported a larger percentage of annual forbs than the adjacent control plots (Fig. 3). This finding suggests that heavy mulch favors cheatgrass and light mulch favors forbs.

Although the two fields were only slightly different in terms of climate and botanical composition, the response to plowing was very different. Plowing greatly enhanced production in the upper field but decreased production on the lower field, at least in 1976.

The data indicate that cheatgrass communities respond to plowing as a soil disturbance by promptly re-establishing the same species composition. Cheatgrass communities, although capable of occupying a site for a long time (decades), are poor in species composition and life forms as compared to stands of the climax *Artemisia tridentata/Agropyron spicatum* association (Daubenmire, 1970). Clearly the inadvertent introduction of cheatgrass and associated annuals to the shrub-steppe region more than a century ago has greatly interfered with the classical secondary succession pattern. With continuous disturbance by man, the role of cheatgrass in plant succession in the shrub-steppe region needs to be realistically evaluated when revegetation of severely disturbed ground is considered in situations other than continuous cultivated agriculture. The data also point out the fact that once disturbed by man's activities, native communities are very slow to return to the site. It is reasonable to expect that if the few remaining stands of native vegetation in the shrub steppe region are not offered some substantial protection, they could also disappear. As stated by Horn (1974), the conscious conservation of climax communities needs to be based upon the idea that climax communities are vulnerable to man's activities rather than

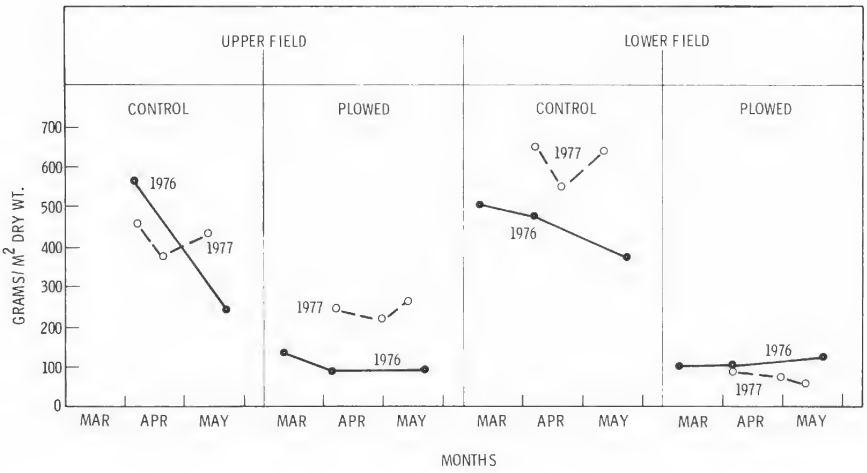

Figure 3. Species composition and contribution (percent) of each species to total live aboveground phytomass in plowed and control plots in cheatgrass communities during the spring of 1976 and 1977 at the upper and lower fields.

inherently stable. The cheatgrass communities are more productive than climax communities (Rickard *et al.*, 1974), at least in terms of aboveground production.

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Plant Associations and Primary Productivity of the Nisqually Salt Marsh on Southern Puget Sound, Washington

Abstract

A study of plant associations and primary productivity was conducted on the salt marsh of the Nisqually River delta located at the southern end of Puget Sound in the State of Washington, U.S.A. Vegetation was sampled along transects placed perpendicular to observed environmental gradients. Twelve plant associations were defined and a vegetation map was prepared showing their extent and location. The distribution of associations appears to be determined by the combined effects of elevation-inundation and the fresh water influence of the Nisqually River. Productivity values were estimated for eight associations using a clip-harvest method, with samples taken at monthly intervals. The average annual net productivity of these eight associations is 814 g dry weight/m^2 with a range of 90 to 1390 g dry weight/m^2. The *Festuca rubra-Carex lyngbyei* association is the most productive of the associations found at high elevations while the *Carex lyngbyei* association, found at low elevations, is the most productive of the associations sampled.

Introduction

Salt marshes are found along both the east and west coasts of North America. On the east coast, salt marsh ecology has been the subject of intensive research. Pomeroy (1959) estimated annual net productivity of benthic algae in Georgia salt marshes. Teal (1962) proposed an annual energy budget for a salt marsh ecosystem in Georgia. Spermatophyte net productivity values have been determined for marshes along the east coast by Steever (1972) and Odum and Fanning (1973).

Until recently, studies of salt marshes on the west coast of North America have been limited and mostly descriptive in nature. Purer (1942) described the vegetation of salt marsh ecosystems along the coast of southern California and discussed the anatomical adaptations of the various species to their environment. Hinde (1954) examined the relation between tidal inundation and distribution of salt marsh vegetation in San Francisco Bay. Macdonald and Barbour (1974) contributed a classification and description of major salt marsh floristic zones from the Aleutian Islands to Baja California. Jefferson (1974) defined plant communities, described their zonation, and investigated several environmental factors influencing plant succession on salt marshes of the Oregon coast. Eilers (1975) estimated net primary productivity of plant communities on a marsh in Nehalem Bay, Oregon, and described community zonation, productivity, and species diversity as they relate to elevation and inundation.

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Crow (1977) described the vegetation of some salt marshes of the Alaska Pacific coast and discussed environmental factors influencing the zonation of plant communities.

To our knowledge, no major studies have been published on salt marshes of the Washington coast. The purpose of our study was to define the plant associations on the salt marsh of the Nisqually River delta and to estimate the annual net primary productivity of these associations.

Study Area

Location. The delta of the Nisqually River is located in Thurston and Pierce Counties, Washington, 16 km northeast of Olympia, Washington (Fig. 1). The delta is a part of the estuary formed by the Nisqually River and McAllister Creek where they enter southern Puget Sound. This area includes salt marsh modified by diking, salt marsh periodically inundated by the tides, and sand-mudflats which extend north to Nisqually Reach. Our study was confined to the undiked salt marsh.

Climate. The Puget Sound area is characterized by a mild, maritime climate including prolonged cloudy periods, narrow diurnal temperature fluctuations, and a long frost-free season. Winters are mild; summers are cool and relatively dry. January mean minimum temperature in Olympia is –0.5°C; July mean maximum temperature is 26.5°C. Mean annual precipitation is 133 cm with 80 percent of this precipitation occurring between 1 October and 31 March (U.S. NOAA, 1974).

Geology. The Nisqually Delta is located in the Puget Trough, a broad structural and topographic depression formed at the time of the final uplift of the present-day Cascade and Coast Range Mountains, 11 million years ago. Repeated glaciation of this area over the past two million years has resulted in the accumulation of large amounts of lacustrine and outwash sediments over the bedrock, as well as a deepening of the northern part of the Trough. Since the last glaciation (the Vashon Stade, 14,000 years ago), the Nisqually River, originating on Mount Rainier, has cut a deep valley into its floodplain. The formation of the present-day delta began about 6000 years ago when sea level attained its present position. During this time the delta advanced northward a distance of at least 2.4 km. It appears to be composed of alternating layers of sand, silt, and clay to a depth of about 42 m (The Nisqually Delta, 1970). Present-day surface sediments are typically black, medium to fine sands. At the present time the delta is thought to be at or near a state of dynamic equilibrium, neither advancing nor retreating (Brundage, 1960).

Description. The Nisqually salt marsh is made up of broad, relatively level, vegetated areas separated by wide drainage channels. These channels were formed, prior to diking, by distributaries of the Nisqually River. Each vegetated area is further dissected by a complex system of winding sloughs (drainage channels) which empty into the main channels and form the intricate drainage patterns characteristic of salt marshes. In the higher, relatively flat parts of the marsh, drainage is restricted to well-developed sloughs up to 2 m in depth. In the lower, gradually sloping vegetated areas, a more diffuse drainage pattern creates a hummocky topography.

Closely associated with the drainage of the salt marsh are salt pans, circular or semi-circular depressions which frequently contain standing water. Four types of salt pan, formed in various ways by vegetation (Chapman, 1964), are present on the

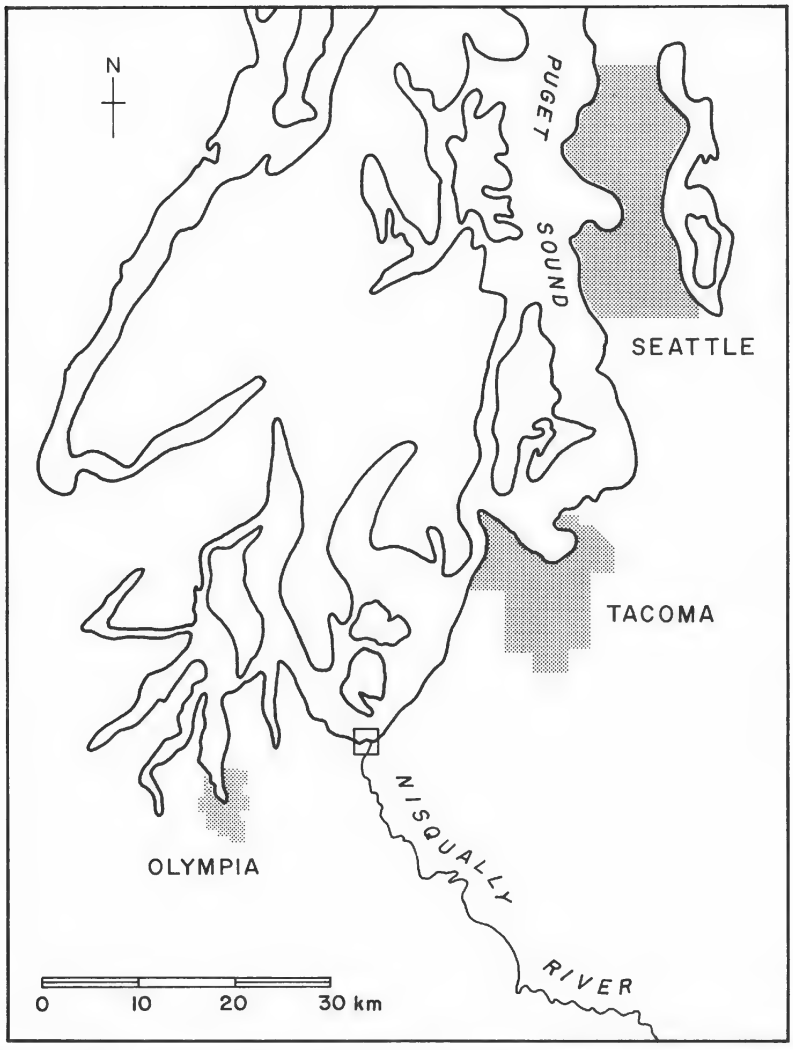

Figure 1. Location of the Nisqually River delta and salt marsh on southern Puget Sound, Washington.

Nisqually marsh. In addition to these we have observed another type of salt pan, commonly inhabited by burrowing Crustacea, which appears to be formed independent of vegetation.

Two types of transition from salt marsh vegetation to unvegetated mudflat characterize the Nisqually salt marsh. The first of these is the gradual slope, characteristic of areas where there is an accretion of sediment or where erosion from upland drainage is not great. The second type of transition is the steep erosion bank. This feature is found where erosion from upland drainage is greater than accretion; it is

restricted to the banks of the Nisqually River and McAllister Creek and areas under the influence of littoral currents.

The Nisqually salt marsh is a complex mosaic of plant communities. The distribution of plant species is determined to a large extent by tidal inundation and factors related to this phenomenon: salinity, water table, nutrient cycling, and aeration. Proximity to fresh water is also an important factor. The zonation of salt marsh vegetation can be traced from the banks of the Nisqually River to the areas farthest from the river's influence. Closest to the river are large expanses of meadow dominated by tussock grasses. In areas bordering the major sloughs near the river are pure stands of sedge. Still farther from the river, there is a transition to zones typified by low-growing forbs and grasses. The lowest elevations throughout the marsh are sparsely vegetated by pioneer species.

Methods

Plant associations. Our study was conducted between April and October 1975. In July, when nearly all species were either flowering or beginning to flower, we recorded species present and estimated their percent areal cover in a total of 138 quadrats along 12 transects placed perpendicular to observed variation in vegetation zonation and apparent salinity and elevation-inundation gradients. The quadrats were placed at 30-m intervals along the transects except in one area of broad zonation in which the quadrat interval was 60 m.

We analyzed the data using an indirect polar ordination method (Bray and Curtis, 1957) based on a species importance value, the cover class midpoint of each species in each quadrat. Four BASIC computer programs were written to perform the required ordination calculations. Co-ordinates for each quadrat were plotted on a two-dimensional graph. Groupings of similar quadrats on the graph were interpreted as representing distinct plant associations.

Primary productivity. Because it was necessary to initiate productivity sampling prior to the sampling conducted to obtain plant association data, sampling sites were located, on the basis of our reconnaissance, in what appeared to be distinct plant communities. Two communities were sampled in May; subsequent sampling at monthly intervals from June through October included eight communities. At each sampling period, three 0.25-m^2 quadrats were subjectively placed in areas representative of each community. All vegetation, both living and standing dead, was clipped to the ground and brought back to the laboratory. Successive samples avoided plots previously clipped. Living and dead material were separated in each quadrat sample, and living vegetation was sorted by species. All material was oven-dried at 100°C for 48 hours, then weighed.

Net aerial primary productivity was estimated by summing peak biomass of individual species in each association and, when possible, biomass lost to death and shedding. No attempt was made to estimate below-ground productivity or biomass lost to tidal export and herbivory. Peak species' biomass was used instead of peak standing crop because species reach peak growth at different times during the growing season. Peak standing crop omits a part of the contribution to annual productivity made by plants maturing before or after peak standing crop is reached and yields a lower estimate (Eilers, 1975). Weights from each of the three quadrat samples taken monthly

TABLE 1. Association table. Average cover (COV) and frequency (FRE) for each of the 24 species characterizing 10 plant associations on the Nisqually salt marsh. (SPMA—**Spergularia marina**; SAVI—**Salicornia virginica**; DISP—**Distichlis spicata**; JACA—**Jaumea carnosa**; CALY—**Carex lyngbyei**; JUBA—**Juncus balticus**; DECE—**Deschampsia cespitosa**; FERU—**Festuca rubra**). (+ indicates less than one percent).

ASSOCIATIONS	SPMA		SAVI		DISP		DISP-SAVI		JACA-DISP		CALY-DISP		DISP-JUBA		CALY-DECE		FERU-CALY		CALY	
No. quadrats	6		2		9		27		34		23		4		13		11		2	
SPECIES	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE
Spergularia marina	97.5	100																		
Salicornia virginica			45.8	100	+	33	37.9	85	18.1	97	4.3	39					+	9		
Agrostis alba			8.5	50			+	3	+	3	1.6	4			11.0	46	3.3	27		
Distichlis spicata					76.3	100	62.6	100	33.9	100	34.6	91	78.9	100	10.0	46	6.6	54		
Triglochin maritimum					+	11	12.2	37	15.4	88	26.8	87	1.8	25	18.6	85	15.8	64		
Carex lyngbyei					+	11	+	7	2.1	30	40.1	100	9.9	50	29.0	100	17.9	73	97.5	100
Grindelia integrifolia					+	11	5.8	18	8.4	70	10.9	78	+	25	+	8				
Jaumea carnosa					+	11	9.6	44	42.9	97	14.8	65	+	25						
Atriplex patula					+	11	+	37	+	70	+	22								
Spergularia canadensis							+	18	+	33										
Cuscuta salina							+	4	6.5	70	+	13								
Glaux maritima							+	7	4.0	70	5.8	96	1.2	50	4.6	77	3.7	64		
Plantago maritima									19.5	79	13.0	65			+	8	+	9		
Juncus balticus									1.1	3	+	4	47.6	100	7.4	62	16.1	54		
Stellaria humifusa									+	9	2.2	61			+	15	+	9		
Hordeum jubatum									+	6	+	4	9.2	25	+	8				
Potentilla pacifica											20.7	74	1.2	50	22.6	92	8.0	82		
Deschampsia cespitosa											+	13	3.5	50	25.4	100	15.5	91		
Hordeum brachyantherum													+	25			+	18		
Lilaeopsis occidentalis													3.4	15						
Aster eatonii													+	8			11.8	64		
Festuca rubra																	82.8	100		
Trifolium wormskjoldii																	1.5	9		
Galium triflorum																	3.4	9		

in each association were averaged to yield one monthly value for each species in each association.

The method used to determine biomass lost to death and shedding was not the same for all associations. Since the dates of maximum production for different species and the effects of tidal inundation vary from one association to another, estimates were based on field observations and data collected for each association.

Results and Discussion

Plant associations. A total of twelve plant associations was identified. Two associations, the *Deschampsia cespitosa-Juncus balticus* association and the *Distichlis spicata-Carex lyngbyei* association, were recognized during the field mapping process. Ordination analysis resulted in the definition of ten plant associations, confirming the eight communities included in our productivity sampling, and revealing two additional associations not recognized during our initial reconnaissance. A list of these ten associations,

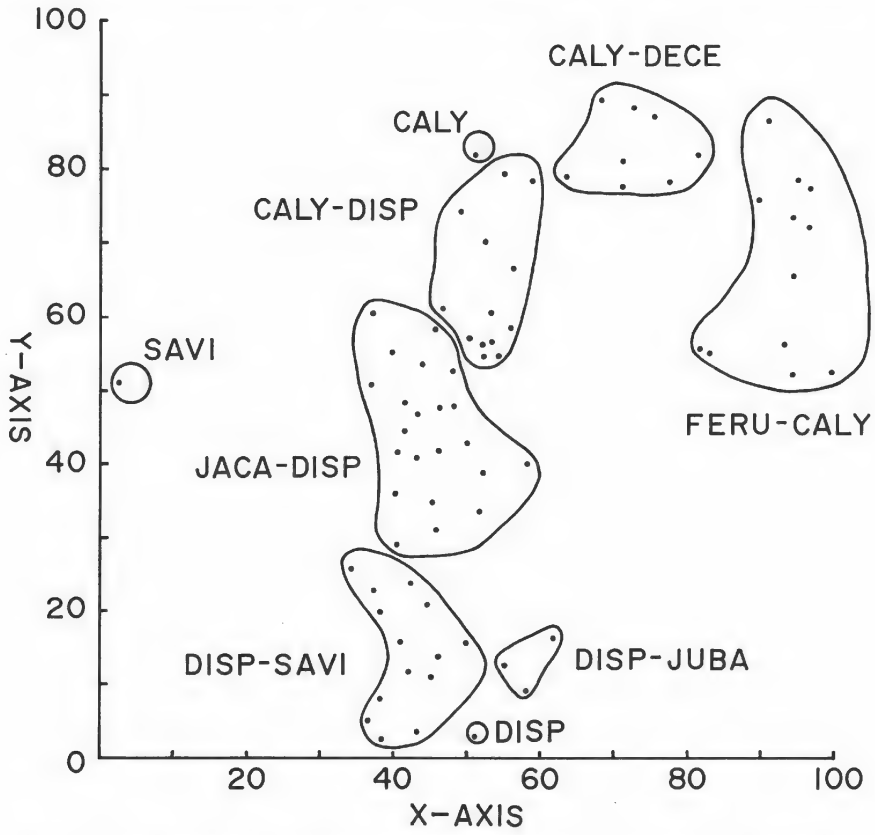

Figure 2. Plotted locations of individual quadrats as determined by computer-aided indirect polar ordination. Distance between points is a function of floristic similarity: the closer the points, the greater the similarity in species composition in terms of species present and their percent areal cover. (For definition of abbreviations, see Table 1.)

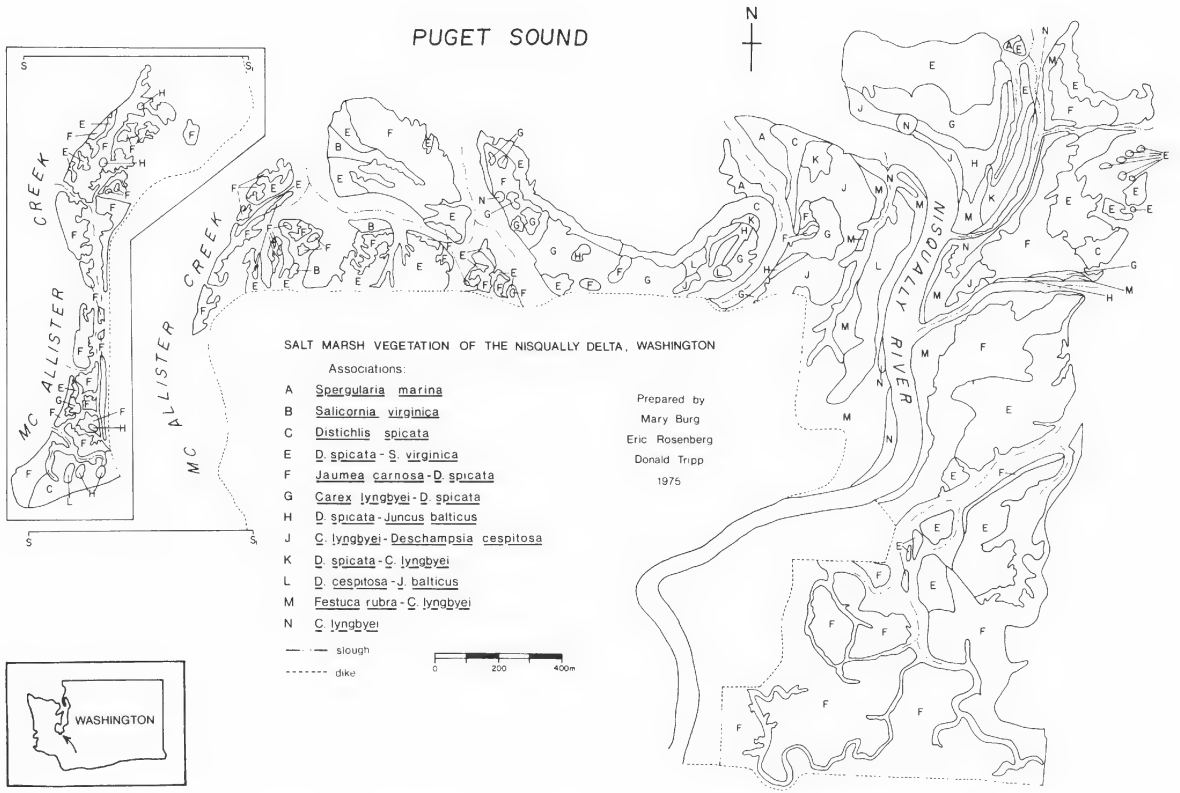

Figure 3. Vegetation map showing the location and extent of the 12 plant associations of the Nisqually Delta salt marsh.

including cover and frequency data for their component species, is given in Table 1. Nomenclature is after Hitchcock and Cronquist (1973).

The quadrat distribution of nine associations is shown on the ordination diagram, Figure 2. The *Spergularia marina* association is not plotted. It is composed of a single species which exhibits a narrow ecological tolerance and which is not present in any other association. Quadrats falling within this association appear totally dissimilar to every other quadrat and cause the remaining quadrats to clump at the opposite end of the axis, complicating further ordination. It was necessary to remove the *S. marina* quadrats before ordination could be satisfactorily completed.

Following is a brief description of each of the twelve plant associations recognized on the Nisqually salt marsh. A vegetation map showing the extent and location of these associations is presented in Figure 3.

1. The *Spergularia marina* association occurs on the gradually sloping transition zones at the lowest elevations on the marsh. *S. marina*, an annual, is the sole species constituting this association. It is a pioneer species which colonizes the mudflat and occurs in no other association. The largest stands are found at the mouth of the Nisqually River. Within the stands, it grows most vigorously adjacent to drainage sloughs and salt pans.

2. The *Salicornia virginica* association is also found at low elevations. Its thickly matted vegetation grows in patches in areas characterized by a diffuse drainage pattern and hummocky topography. It appears to be restricted to a well-drained, well-aerated substrate and is commonly found in soils inhabited by burrowing Crustacea. At the mouth of the river where invertebrate burrows are uncommon, the occurrence of *S. virginica* decreases markedly. Reproduction of this species is largely vegetative, as evidenced by its abundant rhizomes and its patchy growth habit.

3. The *Distichlis spicata* association is confined to low elevations where fresh water influence is present and where decreased aeration of the substrate excludes *S. virginica*. *D. spicata* is the dominant species with the occasional occurrence of *S. virginica* and *Triglochin maritimum*. *D. spicata* has a wide range of ecological tolerance. Capable of reproducing vegetatively or by seed, it is present in nearly every association on the marsh.

4. The *Distichlis spicata-Salicornia virginica* association occupies a habitat intermediate to those characteristic of the *S. virginica* and the *D. spicata* associations. It occurs at low elevations and, in some cases, extends to the margin of the bare mudflat. Vegetation cover is frequently interrupted by the shallow drainage sloughs of the gradually sloping transition zones. *D. spicata* is the dominant, followed by *S. virginica*. A distinguishing feature of this association is the presence of *T. maritimum* in its tussock growth form. Reproduction appears to be predominantly vegetative, though all these species are capable of reproduction by seed. In the spring and summer, tussocks of *T. maritimum* are often draped with mats of brown and green algae.

5. A low, dense, continuous vegetation cover typifies the *Jaumea carnosa-Distichlis spicata* association. It occurs on relatively level areas of the marsh. Its physical appearance is marked by well-developed drainage sloughs up to 1 m deep and the presence of salt pans. A total of 15 species occurs in this association. The characteristic species in order of dominance are *J. carnosa, D. spicata, Plantago maritima, T. maritimum, Grindelia integrifolia, Cuscuta salina*, and *Glaux maritima*. A conspicuous feature of

this association is the concentration of *G. integrifolia* along the tops of slough banks. This species appears to thrive in well-drained areas, and its occurrence is associated with an increase in *S. virginica.* The parasitic spermatophyte *C. salina* is most often found entwining *S. virginica* and *P. maritima.*

6. Dense stands of the *Carex lyngbyei-Distichlis spicata* association occur in the less saline areas of the marsh and are frequently found bordering the upper margins of the *J. carnosa-D. spicata* association. Closer to the Nisqually River, the *C. lyngbyei-D. spicata* association replaces the *J. carnosa-D. spicata* association. The physical appearance is similar to that of the *J. carnosa-D. spicata* association with the addition of *C. lyngbyei* evenly distributed among the other species. Sixteen species are found in this association, the most abundant being *C. lyngbyei, D. spicata, T. maritimum, Potentilla pacifica, J. carnosa, P. maritima,* and *G. integrifolia.*

7. Along the gradually sloping banks of the major sloughs, pure stands of the sedge *Carex lyngbyei* form one of the most interesting associations on the marsh. In this association a tall growth form of *C. lyngbyei* begins its growing season in the fall after most of the previous year's aerial growth has been exported by the tides. At this time, shoots sprout from the rhizomes, remain green all winter, and by May are vigorous and up to 1 m in height. The plants flower in late May and reach a maximum height of 1.5 m by July. Where it occurs in multi-species associations, *C. lyngbyei* seldom exceeds a height of 0.5 m.

Eilers (1975) reported two phases of *C. lyngbyei,* both occurring in pure stands on West Island Marsh in Nehalem Bay, Oregon. One phase, a short growth form, occurs at the lowest elevations (0.77-2.06 m above MLLW). The second phase, a tall growth form (1.8 m or more), grows along sloping banks at elevations between 1.67 and 2.25 m above MLLW. Eilers also observed that *C. lyngbyei* exhibits a slower growth rate in multi-species communities.

8. The *Distichlis spicata-Carex lyngbyei* association is found at low elevations near the Nisqually River. Its lower margins are bordered by the *C. lyngbyei* association or the *D. spicata* association while its upper margins merge with tussock grass meadow vegetation. *D. spicata* and the short growth form of *C. lyngbyei* are co-dominants with a minimal presence of subordinate species. The appearance of this association, both in the field and on aerial photographs, is sufficiently different to distinguish it from any other association on the marsh.

9. The *Distichlis spicata-Juncus balticus* association occurs throughout the salt marsh. In areas closest to the Nisqually River it occurs in bands, bordered on its lower margins by the *C. lyngbyei-D. spicata* association and on its upper margins by the *C. lyngbyei-D. cespitosa* and *Festuca rubra-C. lyngbyei* associations. Farther from the influence of the river, this association occurs in patches up to 50 m in diameter. These patches are surrounded by the *C. lyngbyei-D. spicata* and *J. carnosa-D. spicata* associations. The association is dominated by *D. spicata* and *J. balticus,* followed by *C. lyngbyei* and *Hordeum jubatum,* with minimal amounts of *T. maritimum, P. pacifica* and *G. maritima.*

10. The *Carex lyngbyei-Deschampsia cespitosa* association appears as an area of thick, uniform vegetation cover cut by sloughs up to 2 m deep. The appearance of the area is dominated by the tall tussock grass, *D. cespitosa. C. lyngbyei* and *D. cespitosa*

are co-dominants occurring with *P. pacifica, T. maritimum, Agrostis alba, D. spicata, J. balticus*, and *G. maritima.*

11. The *Deschampsia cespitosa-Juncus balticus* association occupies an intermediate position between the *C. lyngbyei-D. cespitosa* and *Festuca rubra-C. lyngbyei* associations. The species composition and the physical characteristics of this association are similar to those of the *C. lyngbyei-D. cespitosa* association. However, the marked increase in the salt rush *J. balticus* and the decrease in *C. lyngbyei* warrants a distinction between these associations.

12. The *Festuca rubra-Carex lyngbyei* association is restricted to the highest areas immediately adjacent to the Nisqually River and its distributaries. The characteristic species of this association are *F. rubra*, which grows in thick tussocks, *C. lyngbyei, J. balticus, D. cespitosa, T. maritimum, Aster eatonii*, and *P. pacifica.* This association is bordered on its lower margins by the *C. lyngbyei-D. cespitosa* association. When located along major sloughs, its lower margins are bordered by the *C. lyngbyei* association.

Water salinity and elevation-inundation appear to be the two significant environmental gradients influencing zonation of vegetation on the Nisqually salt marsh. Aerial photographs and surface observations indicate that there is a strong westward current at the mouth of the Nisqually River. It is apparent from the map (Fig. 3) that this westward flow of fresh water influences distribution in relation to the above gradients. On the west side of the river, associations in which fresh water influence is significant (A,C,G,H,J,K,L,M,N on the map) generally cover broad areas; associations which are more salt tolerant (B,E,F) are located beyond these, far from the banks and mouth of the river. On the east side of the river, most of the associations greatly influenced by fresh water are restricted to narrow bands along the banks of the river and its major distributaries; the more salt tolerant associations are again located beyond them but much closer to the river than they are on the west side.

From areas near the river to areas farthest from the river's influence, widely different associations occur at identical elevations. For example, on the west side of the marsh along McAllister Creek (which has a negligible diluting effect), elevations as high as 4.8 m above MLLW are occupied by the *J. carnosa-D. spicata* association which is composed of species with high salt tolerances. At the same elevation but closer to the Nisqually River is found the *F. rubra-C. lyngbyei* association, composed of species less tolerant of salinity. These patterns of distribution indicate that the degree of fresh water influence may determine the presence or absence of an association while elevation-inundation determines the vertical distribution of associations within the boundaries set by salinity.

Away from the river's influence, a typical sequence of zonation begins with stands of the *S. virginica* and the *D. spicata-S. virginica* associations adjacent to the mudflats. These stands give way at higher elevations to the *J. carnosa-D. spicata* association with scattered patches of the *D. spicata-J. balticus* association.

At the mouth of the river where salinity is greatly reduced, discontinuous stands of the *S. marina* association occupy the lowest elevations. These stands are bordered on their upper margins by the *D. spicata* association. The occurrence of the *C. lyngbyei* association along the banks of the river and nearby sloughs also marks the decrease in salinity, although the distribution of this association may also be a function of

drainage (Eilers, 1975). At intermediate elevations, stands of the *C. lyngbyei-D. spicata* association are extensive just west of the river mouth and decrease in size and occurrence farther to the west. The highest areas closest to the river are characterized by the *C. lyngbyei-D. cespitosa, D. cespitosa-J. balticus*, and *F. rubra-C. lyngbyei* associations. The individual species which best mark the decrease in salinity by the influence of the Nisqually River are *C. lyngbyei, D. cespitosa, F. rubra, P. pacifica*, and *A. eatonii.*

Primary productivity. Annual net productivity was estimated for eight plant associations: *S. marina, S. virginica, D. spicata-S. virginica, J. carnosa-D. spicata, C. lyngbyei-D. spicata, D. spicata-J. balticus, F. rubra-C. lyngbyei*, and *C. lyngbyei.* Individual species' peak biomass and monthly totals of living and dead material for these associations are presented in Tables 2 and 3, respectively. Estimates of annual net productivity, based on these data, are summarized in Table 4.

Annual net productivity of the *S. marina* association is 90 g dry weight/m^2. This value was obtained from maximum biomass alone. Since this association occurs in the pioneer zone, a salt marsh habitat which is inundated twice daily throughout the year, plant material that dies can be removed by tidal waters within a day. As a result we found no dead plant material in the samples. Fluctuations in monthly samples probably reflect quadrat placement and the scattered growth of individual plants within this association.

The annual net productivity of the *S. virginica* association is 730 g dry weight/m^2. This value was derived from maximum biomass. We did not differentiate between living and dead material since many apparently dead plants (those without leaves) were found to have green vascular tissue. Leaves of *S. virginica* are easily broken off of living plants, and it is likely that the twice daily tides removed this material.

Annual net productivity estimates for the *D. spicata-S. virginica* and the *J. carnosa-D. spicata* associations are 952 g dry weight/m^2 and 800 g dry weight/m^2, respectively. Estimates for both associations were made by computing the difference between values for dead material found in July and August samples and adding this amount to the peak species' biomass total. Peak standing crop for both associations was reached in August; the lowest values for dead material occurred in July. We assumed that any increase in dead material after July was derived from the current year's production.

Annual net productivity for the *C. lyngbyei-D. spicata*, the *D. spicata-J. balticus*, and the *F. rubra-C. lyngbyei* associations is estimated at 908 g dry weight/m^2, 558 g dry weight/m^2, and 1086 g dry weight/m^2, respectively. Because these associations are found at higher elevations where the effects of tidal action are reduced, dead material remains on site for long periods of time. This point is especially true of the *F. rubra-C. lyngbyei* association where, except in the month of July, the amount of dead material present was always greater than that of live material. Since we were unable to determine what proportion of dead material could be attributed to the current growing season, estimates of these associations are based on peak species' biomass alone and are necessarily low.

The annual net productivity of the *C. lyngbyei* association is 1390 g dry weight/m^2. This value was determined by summing weights of living and dead material in July, the time of peak biomass production. In this association all of the previous year's

TABLE 2. Individual species' peak biomass. Shows peak productivity values in dry weight g/m² for each species in each of the eight associations sampled. (M)=month during which individual species reached peak biomass production. (For definition of abbreviations, see Table 1).

ASSOCIATIONS	SPMA		SAVI		DISP-SAVI		JACA-DISP		CALY-DISP		DISP-JUBA		FERU-CALY		CALY	
SPECIES	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)
Spergularia marina	90	(10)														
Salicornia virginica			730	(8)	672	(8)	100	(7)	100	(10)	8	(6)				
Agrostis alba							4	(7)								
Distichlis spicata					270	(7)	68	(8)	110	(8)	52	(7)	66	(7)		
Triglochin maritimum							140	(7)	126	(6)	108	(6)	154	(7)		
Carex lyngbyei							2	(6)	332	(7)			50	(7)	1180	(7)
Grindelia integrifolia											4	(6)				
Jaumea carnosa							370	(8)	116	(9)	34	(7)				
Atriplex patula							2	(7)			2	(6)				
Spergularia canadensis							4	(8)								
Glaux maritima							4	(6)	8	(7)	4	(6)	12	(8)		
Plantago maritima							96	(6)	26	(8)			2	(7)		
Juncus balticus											330	(8)	80	(9)		
Stellaria humifusa									2	(6)			2	(6)		
Hordeum jubatum									2	(6)			14	(6)		
Potentilla pacifica									86	(7)	16	(8)	40	(7)		
Deschampsia cespitosa													344	(10)		
Festuca rubra													322	(6)		
TOTALS	90		730		942		790		908		558		1086		1180	

growth is removed by the tides during the fall of the same year, so any dead material found in July is of the current year's production.

Eilers (1975) estimated annual net productivity for ten of the eleven salt marsh communities on West Island Marsh using the sum of individual species' peak biomass and biomass lost to death and shedding during the current growing season. He reported average net productivity values ranging from 518 g to 1936 g dry weight/m^2. The most productive was the high elevation *Aster-Potentilla-Oenanthe* community which contributed 20 percent of total marsh productivity from 14.7 percent of the

TABLE 3. Average dry weights of live and dead material from the eight associations sampled monthly between May and October. (For definition of abbreviations, see Table 1.)

ASSOCIATIONS	MAY	JUN	JUL	AUG	SEP	OCT
	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2
SPMA						
Live	—	20	20	60	40	90
Dead	—	–0–	–0–	–0–	–0–	–0–
SAVI						
Live	120	170	240	730	530	400
Dead	–0–	–0–	–0–	–0–	–0–	–0–
DISP-SAVI						
Live	120	310	630	920	770	440
Dead	380	310	260	270	260	340
JACA-DISP						
Live	—	410	570	600	370	280
Dead	—	130	100	110	190	170
CALY-DISP						
Live	—	250	720	500	460	260
Dead	—	470	200	240	310	400
DISP-JUBA						
Live	—	470	460	390	280	90
Dead	—	260	210	300	230	330
FERU-CALY						
Live	—	640	560	630	400	360
Dead	—	870	460	840	460	620
CALY						
Live	—	750	1180	740	1020	10
Dead	—	270	210	–0–	–0–	110

TABLE 4. Summary of association and productivity data. Shows the area in hectares and the percentage of total marsh area of each of the twelve associations and annual net productivity in dry weight, total net production (area • productivity), and percentage of total marsh production for the eight associations sampled. (For definition of abbreviations, see Table 1.)

ASSOCIATIONS	AREA		ANNUAL NET PRODUCTIVITY		ANNUAL NET PRODUCTION	
	Total ha	% Total area	g/m^2	kg/ha	Total kg	% Total
SPMA	2.3	1%	90	900	2070	0.1%
SAVI	1.9	1	730	7300	13,870	0.9
DISP-SAVI	47.1	22	952	9520	448,392	26.8
JACA-DISP	86.0	39	800	8000	688,000	41.2
CALY-DISP	15.8	7	908	9080	143,464	8.6
DISP-JUBA	15.6	7	558	5580	87,048	5.2
FERU-CALY	16.2	7	1086	10,860	175,932	10.5
CALY	8.0	4	1390	13,900	111,200	6.7
DISP	8.2	4				
DISP-CALY	2.6	1				
DECE-JUBA	5.6	3				
CALY-DECE	8.9	4				

total area of the marsh. The estimated average net productivity of pure stands of the tall growth form of *C. lyngbyei* was 1746 g dry weight/m^2, a contribution of 12.2 percent to total productivity from an area covering 9.6 percent of the total area of West Island Marsh.

The total dry weight net production of the eight associations sampled on the Nisqually salt marsh is estimated to be 1670 metric tons produced over an area of 192.9 ha. The remaining four associations cover a total area of 25.3 ha. Net production and area of each association are listed in Table 4. These values provide a basis for comparing the contribution of each association to the total productivity of the marsh.

C. lyngbyei is the most productive of the associations sampled. It covers 8 ha, 4 percent of the total area of the marsh, and contributes 6.7 percent of total marsh production. The high elevation *F. rubra-C. lyngbyei* association is the second most productive association, covering 7 percent of the total area of the marsh and contributing 10.5 percent of the total production of the Nisqually salt marsh.

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Some Range Extensions and a New State Record for the Oregon Flora

Abstract

Field studies and herbarium searches in 1977 and 1978 have revealed several plants previously unknown to northeastern Oregon (*Castilleja inverta* (Nels. & Macbr.) Pennell & Ownbey, *Echinocystis lobata* (Michx.) T. & G., *Heuchera rubescens* Torr., *Petasites frigidus* (L.) Fries var. *palmatus* (Ait.) Cronq., and *Polanisia trachysperma* T. & G.), including one species (*Phlox multiflora* A. Nels.) new to the state. Additional locations have also been observed for *Selaginella watsonii* Underw., formerly reported from only one site in Oregon.

Introduction

Northeastern Oregon floristic surveys in 1977 and 1978 have revealed range extensions for several vascular plants. These surveys were conducted in conjunction with threatened and endangered plant inventories. Northeast Oregon, for the purpose of this paper, is considered to include that portion of the state lying north of the 44th parallel which is influenced by the Blue and Wallowa Mountain ranges (Fig. 1). Portions of the Great Basin and Rocky Mountain floras are important elements in this region, with many taxa attaining their northern or western distribution limits here. Four species cited here (*Castilleja inverta*, *Heuchera rubescens*, *Phlox multiflora*, and *Selaginella watsonii*) are plants whose centers of distribution are located within these more southerly and easterly geographic regions. The remaining three species (*Echinocystis lobata*, *Petasites frigidus* var. *palmatus*, and *Polanisia trachysperma*) have general, widespread ranges over much of North America.

Methods

The observations reported in this paper were made during the course of Bureau of Land Management field surveys. Literature and herbarium searches (Humboldt State University-HSC; University of Idaho-ID; University of Oregon-ORE; Oregon State University-OSC; University of Nevada-RENO; University of California, Berkeley-UC; Washington State University-WS; and University of Washington-WTU) were made to substantiate the reported range extensions.

Voucher specimens have been deposited at OSC, ORE, and UNLV (University of Nevada at Las Vegas) for certain of the species listed. A complete set is on file at the Bureau of Land Management herbarium in Baker, Oregon. This herbarium has been tentatively designated by the acronym BKR. Locations of these collections are illustrated in Figure 1. The nomenclature follows Hitchcock and Cronquist (1973).

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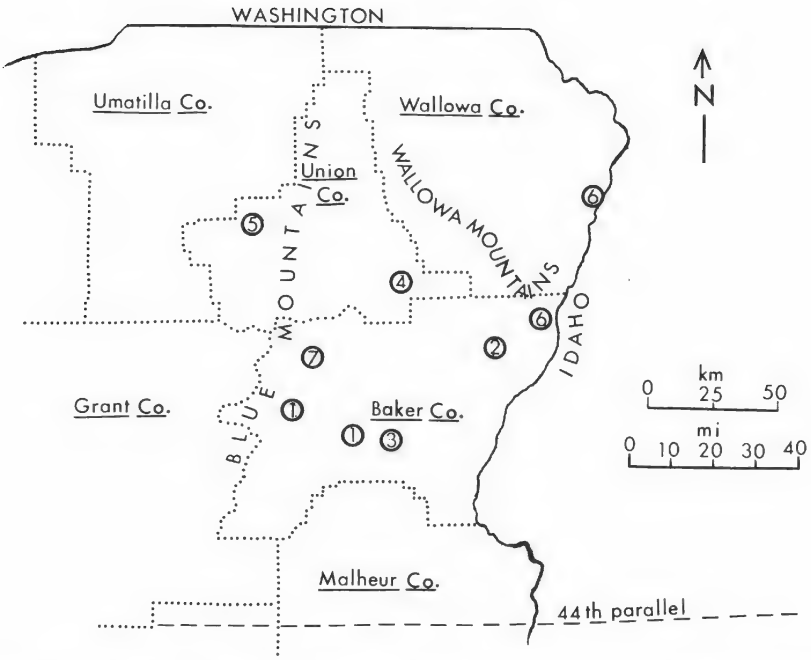

Figure 1. Locations of taxa new to northeast Oregon. 1. *Castilleja inverta* 2. *Echinocystis lobata* 3.*Heuchera rubescens* 4. *Petasites frigidus* var. *palmatus* 5. *Phlox multiflora* 6. *Polanisia trachysperma* 7. *Selaginella watsonii.*

Range Extensions

Castilleja inverta (Nels. & Macbr.) Pennell & Ownbey (Scrophulariaceae) BAKER COUNTY: Approximately 12.0 km south of Baker on State Highway 7, 0.1 km west of the highway on dry, east slope, at 1170 m; May, 1978, Meinke 1893 (OSC). This paintbrush has also been found along State Highway 220, 16.0 km east of Sumpter near the east end of Phillips Reservoir, on exposed rocky slopes, at 1260 m; May, 1978, Meinke 1893a (OSC, BKR). Associate species (both sites): *Pinus contorta*, *Eriogonum sphaerocephalum*, *Juniperus occidentalis*, *Artemisia tridentata*, *Ribes cereum*, *Astragalus curvicarpus*, *Phacelia linearis*, and *Trifolium macrocephalum.*

The previous range of this species has been described as central and southwest Idaho to southeast Oregon and northeast Nevada (Ownbey, 1959; Holmgren, 1973). A collection labeled as *C. pallescens*, June, 1953, Cronquist 7089 (UC), (apparently *C. inverta*; Robert Ornduff, pers. comm.) was taken on a rocky flat near Canyon City, Oregon, in southern Grant County. The Baker County sites are approximately 90 km northeast of the site in Grant County and represent the most northern populations of the species in Oregon.

Echinocystis lobata (Michx.) T. & G. (Cucurbitaceae) BAKER COUNTY: This vine has been found 2.5 km northeast of Halfway, on dense vegetation bordering East Eagle Creek, at 845 m; August, 1978, Meinke 2230 (BKR). Associate species: *Rosa nutkana*,

Geum aleppicum, *Prunus virginiana* var. *melanocarpa*, *Salix amygdaloides*, *Crataegus columbiana* var. *piperi*, *Cicuta douglasii*, and *Mentha arvensis*.

The range of *E. lobata* has been variously described as common in the eastern and southern United States, then west to Montana (Cronquist, 1959, 1973); from the eastern United States to southern Idaho (Davis, 1952); and from the eastern United States westward as an escape to the Willamette Valley of Oregon as well as eastern Washington and western Idaho (Ferris, 1960). Only one herbarium specimen from Oregon, labeled August, 1915, Gorman 3616 (WS), could be located in a search of major Pacific Northwest herbaria. This collection would certainly seem to be a waif although it is unknown whether the Baker County collection is an escape or from a native population, due to the relatively undisturbed habitat. At any rate, this is the first positive record of the species from east of the Cascades in Oregon, and the only recent record for the state.

Heuchera rubescens Torr. (Saxifragaceae) BAKER COUNTY: Found 12.0 km northeast of Bridgeport, along the Burnt River, on high, shaded cliffs, at 985 m; May, 1978, Meinke 1882 (OSC, BKR). Associate species: *Penstemon deustus*, *Heuchera cylindrica*, *Clematis ligusticifolia*, *Cirsium utahense*, and *Haplopappus resinosus*.

H. rubescens is well known from the Great Basin, the Sierra Nevada (Hitchcock, 1973; Abrams, 1944; Davis, 1952; Munz, 1959), and from much of the Mohave Desert of California, Arizona, and Nevada (Patrick Leary, pers. comm.). In southeast Oregon, the species has been collected numerous times on Steens Mountain (collections at UC, WS, and OSC) as well as near Van Horn Creek, five miles north of Denio, in May, 1959, Cronquist 8310 (UC, ID). The collection along the Burnt River was made approximately 200 km north of the previously known northern extent of the species in Oregon and is possibly the farthest north it has yet been reported.

Petasites frigidus (L.) Fries var. *palmatus* (Ait.) Cronq. (Compositae) UNION COUNTY: An intermittent colony of this plant stretches from 5.0 to 9.0 km east of State Highway 237 along Forest Service Road S550, on banks and flats adjacent to or above Catherine Creek, in the western foothills of the Wallowa Mountains, at 1140 m; August, 1978, Meinke 2228 (OSC, BKR). Associate species: *Alnus sinuata*, *Mimulus guttatus*, *Rhamnus alnifolia*, *Pteridium aquilinum*, *Athyrium filix-femina*, *Equisetum hyemale* var. *affine*, and *Ranunculus sceleratus*. The colonies presently consist of several hundred individuals. The positioning of Forest Service Road S550 has considerably reduced the population from its original size.

P. frigidus var. *palmatus* is a circumboreal species which extends across Canada and south at irregular points into the United States. In the western United States it is known from the Cascade crest to the coast (Ferris, 1960; Cronquist, 1955, 1973) and from the Coast Ranges as far south as Monterey County, California (Munz, 1959). The Catherine Creek population represents a considerable disjunction, at least 320 km from the nearest known site in the Cascades. It is puzzling that no collections of this plant have been previously reported from this locale, considering the amount of botanical exploration that has been conducted in the nearby Wallowa Mountains.

Phlox multiflora A. Nels. (Polemoniaceae) UNION COUNTY: This species was col-

lected approximately 10.0 km south of Interstate 80-North, along State Highway 244 on cliffs east of the Grande Ronde River, at 975 m; May, 1977, Meinke 1473 (ORE, BKR). Associate species: *Cirsium brevifolium*, *Alnus rhombifolia*, *Silene douglasii*, *Heuchera cylindrica*, *Lupinus laxiflorus*, *Penstemon deustus*, and *Cystopteris fragilis*.

P. multiflora ranges the northern Rocky Mountain states to Nevada and New Mexico (Cronquist, 1959, 1973; Davis, 1952; Harrington, 1954). This phlox has been reported only as far west as central Idaho and northeast Nevada (Davis, 1952). The population along the Grande Ronde River is isolated approximately 250 km to the west from the previously suspected western limits of the species. The identity of this collection has been verified by comparison with material from ORE annotated by Edgar Wherry (David Wagner, pers. comm.). This is the first record of this plant from Oregon or the Pacific states.

Polanisia trachysperma T. & G. (Capparidaceae) WALLOWA COUNTY: Found near Waterspout Rapids, Snake River, on a "rocky shingle below high water line along river"; August, 1974, F. D. Johnson (ID). BAKER COUNTY: This species was growing 6.0 km southwest of the Snake River on a dry hillside between State Highway 86 and Pine Creek, at 585 m; June, 1977, Meinke 1541 (UNLV, BKR). Associate species: *Cryptantha torreyana*, *C. celosioides*, *Sisymbrium altissimum*, *Mimulus nanus*, *Perideridia bolanderi*, *Bromus tectorum*, and *Purshia tridentata*.

P. trachysperma is widespread from southeast Oregon and northeast California to Arizona and Texas (Cronquist, 1964, 1973) and south into Mexico (Munz, 1959). It is also known from across western Canada to Saskatchewan, south through the midwestern United States into Alabama (Davis, 1952). With the exception of Johnson's collection in 1974, the species in Oregon is scantily represented in local herbaria, and then only from the southeast portion of the state. These two collections verify the extension of this plant's range into northeast Oregon.

Selaginella watsonii Underw. (Selaginellaceae) BAKER COUNTY: Found 0.5 km south of Willow Creek Lake on granodiorite talus, in the Blue Mountains (Elkhorn Ridge), at 2450 m; August, 1977, Meinke 1724 (ORE). Also found on the north slope of Hunt Mountain, on a rocky crest approximately 1.6 km east of Willow Creek Lake, at 2430 m; August, 1977, Meinke 1724a (BKR). Associate species: *Bupleurum americanum*, *Phyllodoce empetriformis*, *Claytonia megarhiza* var. *bellidifolia*, *Sedum roseum*, and *Collomia debilis*.

S. watsonii is found in the southern Great Basin and Mohave Desert, with isolated stations known from southwest Montana and another from the Wallowa Mountains (Union County) in northeast Oregon (Cronquist, 1969, 1973; Munz, 1959; Taylor, 1970; Maxon, 1923). The two sites observed in the Blue Mountains are approximately 50 km west of the populations in the Wallowas and thus expand the range of this plant in the Northwest. This plant has been recognized as rare and possibly threatened in Oregon (Siddall et al., 1979).

Discussion

Seven plant species have been presented here as new constituents of the northeast Oregon flora. These records are all of disjunct populations of species which are common in other

areas. One, *Phlox multiflora*, is disjunct in Oregon from a major population center outside the state. The other species mentioned have at least a portion of their primary ranges within Oregon. Three of the plants discussed in this paper (*Petasites frigidus* var. *palmatus*, *Phlox multiflora*, and *Selaginella watsonii*) have populations which are isolated enough to merit special attention with regard to natural resource management.

Disjunct populations are those which are biogeographically segregated from the major distribution centers for the respective species. Of the seven disjuncts discussed here, only one, *Selaginella watsonii*, is currently identified as possibly threatened in Oregon because of its limitation in the state to very local populations. A similar case arose when *Bupleurum americanum* (Umbelliferae) was first reported from Oregon (Meinke, 1978) and placed on the state list of threatened and endangered candidates. *Phlox multiflora*, also a "new" species for the state, will presumably be listed as a possibly threatened or endangered plant as well. Preserving such outlying populations is desirable, as they may be of possible interest to plant geographers and taxonomists interested in floristics or speciation. Designating these populations as "rare, threatened, or endangered" brings them to the attention of the agencies and individuals responsible for land management decisions; it should thus facilitate their conservation. *Selaginella watsonii*, *Bupleurum americanum*, and *Phlox multiflora* are species which are known primarily from outside Oregon, so it is easy to rationalize their inclusion on the list of rare taxa for the state. Under current practice, however, species with disjunct populations which do not happen to cross the state line are not eligible for addition. This practice is unfortunate, since the isolation of a species by biogeographic barriers is of equal interest whether on an interstate or intrastate level. *Petasites frigidus* var. *palmatus* is certainly not threatened in western Oregon, but it is extremely rare east of the Cascades. The disjunct population of this plant near the Wallowa Mountains deserves consideration in management but may not receive it without some type of official status.

The addition of a population to a list of sensitive taxa should be determined on an individual basis, irrespective of whether the particular species is rare within the state. The criteria used in evaluating additions to the state rare and endangered lists need to be expanded to allow the inclusion of intrastate disjunct populations which may conceivably prove to be taxonomically distinct. For example, the extirpation of a colony of *Hackelia hispida* var. *hispida*, a locally common regional endemic recognized as threatened by the federal government (U.S. Department of the Interior, 1975), although undesirable, would not seem as great a scientific loss as the destruction of the only known population of *Petasites* east of the Oregon Cascades. Although the *Hackelia* is an endemic, a single population could be considered expendable when compared to the *Petasites* population which may be one of a kind. It cannot be currently stated that this particular *Petasites* population is indeed genetically divergent from those elsewhere, but it is known that geographic isolation of plants is a key factor in speciation, allowing new evolutionary lines to be built up and maintained. The assumption cannot always be made that populations of species showing disjunct distribution are in fact the same, since relatively few comparative studies have been made. Subtle differences in ecology, such as climatic or edaphic factors, may be sufficient to initiate the divergence of a population (Davis and Heywood, 1973). The differences in climate between the Wallowas and Oregon west of the Cascades are considerable.

The *Petasites* example illustrates the need to examine rare plants as potential candi-

dates for protection at other than simply the recognized species level. Many of these rare populations occur on government lands. The need for their inclusion on some "official" list is obvious, considering that many state and federal agency offices have demonstrated reluctance in the past to manage for rare species in lieu of a document specifically requesting such action. Without the enlightenment and cooperation of these agencies, efforts to maintain rare populations or restricted species cannot be successful.

Three of the seven disjunct populations reported in this paper can be considered unique, or "rare," in Oregon. Two of these (*Selaginella watsonii* and *Phlox multiflora*) are recognized under current schemes of classifying rare plants in Oregon, and the third (*Petasites frigidus* var. *palmatus*) under a modified view allowing the inclusion of disjuncts which may possibly be genetically divergent, regardless of whether they occur in an inter-or intrastate pattern. It will not be easy to conclude what populations to include in this category, which to exclude: avoiding arbitrary decisions will often be difficult. But this aspect in rare and endangered species management is nonetheless an important one and should not be disregarded.

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Erratum

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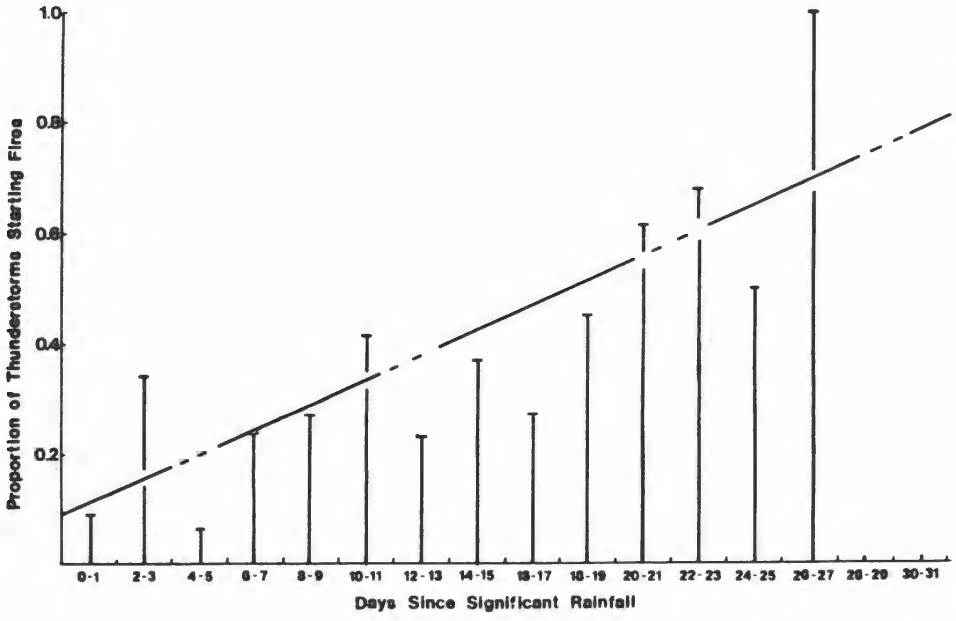
Figure 3 should be as below: legend is correct as published.



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American Coot Nesting and Feeding Habits in Southeastern Washington[1]

Abstract

Nesting and food habits of the American Coot (*Fulica americana*) were studied on the Department of Energy's Hanford Site and Columbia National Wildlife Refuge in Southeastern Washington from 1974 through 1976. Among differences between sites was the presence of low levels of radionuclides on the Hanford Site derived from nuclear fuel reprocessing. Similarities among all nesting habitat were stable water level, moderate to shallow water depth, and emergent aquatic plant communities of cattail and bulrush. Nests found from April through mid-June contained an average of 6.7 eggs per nest. Hatching success was similar at both study sites. Differences found in food habits between study areas were probably related to availability of food items in each pond.

Introduction

The feeding and nesting habits of the American Coot (*Fulica americana*) were studied from 1974 through 1976. Ponds of similar vegetational succession stages and water depth were selected for investigation. These were Gable Mountain Pond, U Pond, and B Pond on the U.S. Department of Energy (DOE) Hanford Site, and Royal Slough, Morgan Lake, and Halfmoon Lake within the Columbia National Wildlife Refuge (NWR) located 15 km north of Othello, Washington. The Hanford site ponds differed from the NWR study ponds, having received small amounts of radionuclides and other contaminants introduced along with process water from nuclear fuel reprocessing facilities.

The objective of this study was to observe possible differences in the nesting biology of coots residing on the contaminated ponds of the Hanford Site and those nesting on the ponds of the Columbia National Wildlife Refuge. Biological features examined were diet, nesting habitat and nest site selection, duration of egg laying and incubation, clutch size, egg and chick weight, and overall nesting success (productivity).

Study Areas

The study areas consisted of shallow ponds, three located on the Hanford site and three

[1]Work was performed for the U.S. Department of Energy under Contract EY-76-C-06-1830 and in cooperation with the Columbia National Wildlife Refuge.

on the Columbia NWR. The Hanford Site ponds were created to contain liquid waste from nuclear fuel reprocessing facilities (Table 1).

Gable Mountain Pond is the largest of the ponds studied. The water source is primarily coolant water which is discharged continuously. The pond is partly dike-constructed and has not been treated with herbicides to control riparian vegetation. Dense stands of cattails and bulrushes occur around the shoreline and as three island-like patches distributed throughout the pond.

B Pond receives water from a coolant source and a chemical sewer. Shoreline dike construction and herbicide applications in 1971 and 1972 destroyed most riparian and emergent aquatic plants. Some isolated bulrush and cattail patches occur in the pond, but the shoreline is ringed by a narrow zone of barnyard grass. A few willows less than 2 m high occupy one end.

U Pond has received coolant water and other waste water since July, 1944. There was no control of plant growth until July, 1972 when a chemical herbicide was applied which defoliated approximately 80 percent of the cottonwoods and willows. Other species, both terrestrial and aquatic, were less affected. Some of the trees, mostly cottonwoods, showed new growth by the next spring with final recovery of about one-half of the original live canopy cover.

Natural ponds studied on the Columbia NWR were Morgan and Halfmoon Lakes and Royal Slough (Table 1). Morgan and Halfmoon Lakes are connected by a channel. Basalt outcroppings and cliffs form parts of their shorelines. Bulrushes form island-like patches throughout the marshy Royal Slough.

Most of the nesting study data were collected from Gable Mountain Pond and the three ponds on the Columbia NWR. Food study data were collected from all ponds.

Methods and Materials

Visits were made nearly weekly to Gable Mountain Pond, Morgan Lake, Halfmoon Lake, and Royal Slough from late March through July of 1976. Nests were discovered by systematic searching while canoeing and wading. Data recorded included the number of eggs and young present, weight of eggs and young, nest location, cover type, and nest fate. Eggs were counted in each nest during each visit and the date of initiation of laying was estimated by allowing one egg per day (Sooter, 1941; Gullion, 1954). Nests were marked with individually numbered pieces of orange plastic flagging tape tied to nearby vegetation.

For dietary information, coots were collected (by shooting) monthly in 1975 and 1976. The proventriculus and gizzard contents were saved for food habit analysis. Few food items were present in the proventriculi, but most gizzard samples did contain food fragments. The gizzard contents were separated into food and grit by washing with distilled water. Two slides from each gizzard sample were prepared with Hoyer's solution (Hansen and Flinders, 1969) and dried for approximately 72 hr at 60°C. Plant fragments were identified by microscopic examination of epidermic cells. Reference material prepared from plant specimens collected in the study area aided in identification. Twenty microscope fields were examined on each slide and all recognizable fragments recorded. Frequency of occurrence was measured by dividing the number of microscope fields in which a given species occurred by the total number of views x 100 (Curtis and

TABLE 1. Historical and biological information concerning study areas.

Location and pond name	size (ha)	Age year	Date Initiation	Average depth	Dominant emergent aquatic plants	Dominant submergent aquatic plants	Adjacent shoreline vegetation
Hanford Site							
Gable Mountain Pond	29	17	1957	1.6	Cattail (**Typha latifolia**) Bulrush (**Scirpus acuta**)	Pondweeds (**Potamogeton Spp.**)	Big sagebrush (**Artemisia tridentata**) with understory of cheatgrass (**Bromus tectorum**) and Sandberg bluegrass (**Poa sandbergii**) (Cline et al., 1977).
B Pond	19	29	1945	3	Bulrush (**Scirpus acuta**)	Pondweeds (**Potamogeton Spp.**)	Russian thistle (**Salsola kali**) and cheatgrass and barnyard grass (**Echinochloa crus-galli**)
U Pond	6	30	1944	1.5	Bulrush (**Scirpus acuta**) and sedges (**Carex** spp.)	Pondweeds (**Potamogeton Spp.**) and duckweed (**Lemna minor**)	Cottonwoods (**Populus** sp.) and willows (**Salix amygdaloides**) Russian knapweed (**Centurea repens**) and cudweed (**Graphalium margaritacea**)
Columbia NWR							
Morgan Lake	13	—	—	3	Cattail and Bulrush	Pondweeds	Big sagebrush-cheatgrass-Sandberg bluegrass
Halfmoon Lake	6	—	—	1	Cattail and Bulrush	Pondweeds	Big sagebrush-cheatgrass-Sandberg bluegrass
Royal Slough	24	—	—	1	Bulrush	Pondweeds	Big sagebrush-cheatgrass-Sandberg bluegrass

McIntosh, 1950). This value of frequency for a given species was divided by the total of the frequency values for all species and expressed as relative percent frequency.

Results and Discussion

Nesting Habits and Clutch Sizes

All ponds had stable water levels and moderate to shallow (1 to 3 m) depths. Shorelines supported cattail-bulrush communities. These features appear to be important for coot nesting; in particular, cattails and bulrushes serve as nesting and rearing cover.

Nests were floating platforms of cattails and/or bulrushes woven around standing vegetation (Fig. 1). Fifty (76 percent) of the study nests were situated in bulrush (*Scirpus*) stands and 16 (24 percent) in cattail (*Typha*) habitat. A summary of coot nest locations is shown in Table 2.

TABLE 2. Vegetation occurrence and use at coot nesting sites.

Study Area	Vegetation	approximate % occurrence	number of nests	% occurrence
Gable Mountain Pond	**Typha** (cattail)	60	9	64
	Scirpus (bulrush)	40	5	36
Royal Slough	**Scirpus** (bulrush)	100	24	100
Morgan and Halfmoon Lake	**Typha** (cattail)	40	7	25
	Scirpus (bulrush)	60	21	75

Nests containing eggs were observed from mid-April to mid-June, 1976. Guillion (1954) reported that the American Coot lays one egg a day with clutches containing from four to ten eggs. Our data appear to support his findings. Coots we observed finished egg laying in mid-May. Nests with eggs observed in mid-June were thought to be renestings after loss of initial clutch.

We examined 66 coot nests during the course of this study and found 41 used for egg laying. Eleven nests were examined on Gable Mountain Pond, 13 on Halfmoon and Morgan Lakes, and 17 on Royal Slough. The mean clutch size was 6.71 $\pm$ S.E. 0.49. We compared clutch sizes among areas using an ANOVA test and found no significant differences $\alpha = 0.05$. Clutch size data collected in our study are compared to data from other North American areas in Table 3. Clutch sizes of the American coot in southeastern Washington appear to be smaller than those reported in other studies. The reasons for this are presently unclear. Our sample size of 41 clutches may not be ade-

TABLE 3. Clutch sizes of the American Coot.

Number of Clutches	Clutch size	Mean	Location	Reference
11	3-10	6.45	Gable Mountain Pond	Present study
13	1-11	6.08	Morgan and Halfmoon Lakes	Present study
17	1-12	7.35	Royal Slough	Present study
41	1-12	6.71	All ponds	Present study
169	5-13	9.9	Manitoba	Kiel (1955)
104	1-11	6.08	Iowa	Sooter (1941)
347	4-18	7.92	Iowa	Sooter (1941)
281	4-17	9.03	Iowa	Fredrickson (1967)
8	7-10	9.0	California	Gullion (1954)
5	4-8	6.4	California	Gullion (1954)

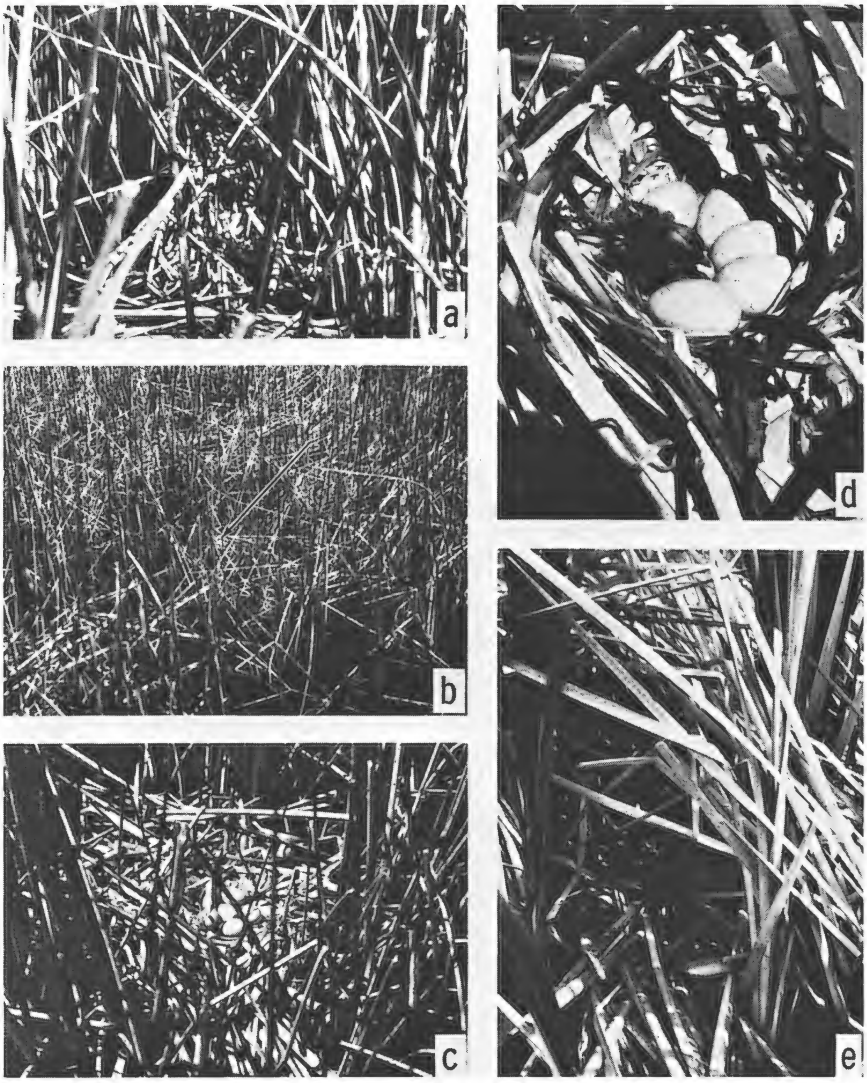

Figure 1. Typical nest structures of the American Coot. a. Approach ramp to nest in bulrush habitat; b. Nest concealed in typical bulrush habitat; c. Clutch in bulrush nest; d. Newly hatched chick in cattail nest; and e. Nest hidden by a dense canopy of cattails.

quate for comparison purposes. Differences may simply reflect population variation in different geographical areas. Clutch sizes reported in this study may not represent the actual (maximum) clutch size because eggs which were destroyed or lost between surveys could not be used in computing clutch size. The mean clutch sizes reported in this study, therefore, represent the minimum clutch size as influenced by natural egg losses

during laying. Table 4 presents the frequency distribution of clutch sizes. These data reveal that clutches from 6 to 10 eggs are most common.

TABLE 4. Distribution of clutch size in the American Coot study areas-1976.

Clutch Size	Gable Mountain Pond	Morgan and Halfmoon Lakes	Royal Slough	Total
1	0	2	3	5
2		1		1
3	1			1
4		1		2
5	1			1
6	5	2	2	9
7	1	1	1	3
8	2	1	5	8
9		2	1	3
10	1		3	4
11		2		2
12			2	2

Egg and Chick Weight

Eggs from a pond in each study area were weighed in May, 1976. Results are shown in Table 5. These data are similar to those reported by Gullion (1954) in California. There are no significant differences in egg weights among coots on Gable Mountain Pond and Morgan Lake and the California birds. We did not statistically compare egg weights among study areas, since expected variations can be accounted for as a function of weight loss through incubation time. Ranges in egg weights do show that there are no gross differences in egg weights among study areas.

TABLE 5. Comparison of weights of American Coot eggs from two study areas.

	Number nests	Weight, g average	range
Gable Mountain Pond (30 eggs) May 12, 1976	4	31.62 ± 0.51	27.2 – 37.0
Morgan Lake May 22, 1976	1	30.8 ± 0.43	29.0 – 32.0
	1	31.0 ± 0.27	30.0 – 32.0
	1	30.0 ± 0.27	28.0 – 31.0
Morgan Lake May 29, 1976	1	29.6 ± 0.41	28.0 – 31.0
(Same eggs as above)	1	29.6 ± 0.24	28.0 – 31.0
	1	28.0 ± 0.24	26.0 – 29.5

Pipping eggs had a mean weight of 25.65 g ± S.E. 0.58 (N = 13). Gullion (1954) provides similar data. As eggs approached the hatching date, they lost weight, which is a common phenomenon in birds. Six chicks weighed immediately after hatching had a mean weight of 19.97 g ± S.E. 0.44 (range 18.5 -21.3 g). Gullion (1954) reported the weight of a newly hatched chick as 22.4 g.

Hatching

The first hatching we observed occurred on Gable Mountain Pond on 12-13 May. The

peak period for hatching on all ponds was approximately 8 June, although a small number of eggs hatched after 20 June. In the 41 nests examined for hatching success (Table 6), only four infertile eggs and no dead embryos were found. Three infertile eggs were found in a clutch of six eggs and one was found in a clutch of eight eggs, both from Royal Slough. Successful nests usually hatched all eggs; unsuccessful nests usually resulted from loss of an entire clutch.

TABLE 6. Percentage of successful American Coot nests.

Nests Number	% Success	Location	Reference
66	92	Washington	Present study
14	100	G. M. Pond	Present study
17	89	Royal Slough	Present study
13	92	Morgan and Halfmoon Lakes	Present study
104	91	Iowa	Sooter (1941)
347	77	Iowa	Sooter (1941)
380	97	Manitoba	Kiel (1955)
161	86	Iowa	Fredrickson (1967)

Food Habits

The gizzard contents of 95 adult and 48 juvenile coots were analyzed. Eighty-nine coots were collected from Gable Mountain Pond, 25 from B Pond, 14 from U Pond and 15 from the NWR. Vegetable material made up 79 percent of the food eaten by the juveniles and 89 percent of the food eaten by the adults (Table 7). The most common plants eaten were pondweeds, water milfoil (*Myriophyllum* sp.), and filamentous algae.

TABLE 7. Food of the American Coot in Southeastern Washington.

	Plants	% Frequency ± S.E. Juvenile Diet N = 48	% Frequency ± S.E. Adult Diet N = 95	Total
Plants	Thallophyta			
	Algae			
	Filamentous algae	18.2 ± 0.3	22.5 ± 0.2	21.2 ± 0.2
	Chara sp (muskgrass)	1.6 ± 0.1	4.5 ± 0.2	3.7 ± 0.1
	Spermatophyta			
	Najadaceae			
	Potamogeton sp (pondweed)	22.5 ± 0.3	21.2 ± 0.2	21.2 ± 0.2
	Potamogeton pectinatus (Sago pondweed)	19.5 ± 0.5	16.7 ± 0.3	17.2 ± 0.3
	Cyperaceae			
	Scirpus sp (bulrush)	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
	Lemnaceae			
	Lemna sp (duckweed)	0.5 ± 0.4	0.5 ± 0.2	0.5 ± 0.2
	Typhaceae			
	Typha latifolia (cattail)	0.6 ± 0.3	0.5 ± 0.2	0.5 ± 0.2
	Ranunculaceae			
	Ranunculus aquatilis (white water crowfoot)	0.2 ± 0.2	2.9 ± 0.2	2.1 ± 0.5
	Haloragidaceae			
	Myriophyllum sp (watermilfoil)	14.0 ± 0.4	17.0 ± 0.2	17.2 ± 0.2
	Undetermined vegetation	2.2 ± 0.1	2.7 ± 0.2	2.5 ± 0.2
Animals				
	Invertebrates	20.5 ± 0.5	11.1 ± 1.6	13.6 ± 0.2

Animal materials (Odonata, Diptera, Coleoptera, Hemiptera) made up 21 percent of the food eaten by juveniles. Juvenile coots from 1 to 120 days of age were pooled in our dietary analysis and hence our values very probably underestimate the true importance of invertebrates to birds from 1 to 30 days old. Sooter (1941, p. 91) states that "animal food material was evidently of more importance with the youngest coots, for older juveniles and adults had eaten only a small percent of this type of food."

No vertebrate remains were found in any of the coot stomachs we examined, although we did observe adult coots feeding on goldfish at Gable Mountain Pond. However, in view of our analyses of the stomach contents of 143 coot and the known feeding habits of the species, it appears unlikely that coots consume many fish.

Our study reflects changes in food habits of the coot on the Hanford Site since the 1950s. Hanson and Browning (1957) did not find pondweeds in their dietary analysis of coots inhabiting ponds on the Hanford Site. In the late 1950s, the ponds (Fitzner and Price, 1973; Fitzner and Rickard, 1975) were relatively new and pondweeds had not yet become established. Gable Mountain Pond was not even created until 1957. At that time, smartweed (*Polygonum* spp.), bulrush, and wild millet (*Echinochloa* sp.) were present and served as food for the coot. Table 7 lists the food consumed in 1976 by coots in the study areas. The ponds on the Hanford Site have abundant algae because there is no outflow, but the ponds of the Columbia Wildlife Refuge have little algae because there is some water flow. Since coots are fairly opportunistic in their selection of foods (Sooter, 1941), we assume that they would eat food in proportion to its availability. Our food habit analyses confirm the findings of Sooter (1941), Jones (1940), Hanson and Browning (1957), and Eley and Harris (1976), which reported that coots feed primarily on plant materials. Sooter (1941) and Jones (1940) noted that animal foods were more important to juvenile coots than adults.

Our studies of the American coot show that the differences in feeding and nesting habits among sites result from differences in availability of food and cover as they do in other studies in the United States and not from the presence of waste in the manmade ponds.

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Importance of Insects and Zooplankton in the Diet of 0-Age Chinook Salmon (Oncorhynchus tshawytscha) in the Central Columbia River

Abstract

Feeding habits of 0-age chinook salmon (*Oncorhynchus tshawytscha*), collected in the Hanford Reach of the Columbia River, were evaluated from March through July, 1976. Food items in chinook guts were compared to potential food organisms in the Columbia River.

Aquatic insects formed the bulk of the diet. Midge fly (Chironomidae) larvae and pupae accounted for 78 percent by number and 59 percent by volume of the total ingested items. Consumption of immature insects was greatest during March-June, whereas caddisfly adults were important food items in June and July. The cladoceran, *Daphnia schødleri*, was numerically and volumetrically important during the latter part of the study period. There was little size-related difference in diet, although chinook fry longer than 66 mm (FL) preyed mainly on caddisfly adults (7 percent number, 64 percent volume) and cladocerans (70 percent number, 13 percent volume). Chironomidae larvae dominated benthic samples in April and June with Trichoptera larvae in lesser abundance. Midstream zooplankton tows collected primarily Copepoda.

Introduction

Several studies (Gerke and Kaczynski, 1972; Carlson, 1976; Craddock *et al.*, 1976) indicated the importance of crustacean zooplankton in the diet of juvenile Pacific salmon (*Oncorhynchus* spp.) residing in semi-estuarine or marine environments. In contrast, studies in freshwater lotic environments showed that although zooplankters are sometimes abundant in river drift, insects formed the bulk of juvenile chinook salmon diet (Chapman, 1938; Becker, 1970, 1973; Sasaki, 1976). Although Becker (1970, 1973) previously described feeding habits of fall chinook salmon fry at Hanford, additional studies were needed to compare chinook diet to potential food organisms present in the Columbia River. This paper describes seasonal and size-related feeding differences in the diet of chinook salmon fry captured in nearshore habitats of the Columbia River. Data on relative abundance of zooplankton and benthos during the period of fall chinook fry residence are included.

Methods

Newly emergent fall chinook salmon fry reside in the Hanford stretch of the Columbia River from March through July. During the 1976 outmigration, fish were collected weekly by beach seine at eight stations between Columbia River kilometer 557 and 613. Collected fish were immediately preserved in 10 percent Formalin. Fork length (FL) and weights of preserved fish were recorded in the laboratory. Stomachs were later removed and contents were washed into shallow dissecting pans. Food organisms were

sorted using a binocular microscope, identified to the lowest practical taxon, characterized by developmental stage, and enumerated. Food items were distributed to a uniform depth and visual volume estimates were made using grids (Windell, 1970). The number of stomachs containing each food item was recorded and expressed as a percentage of the total number of stomachs examined. Relative importance of food items was analyzed by month and by size of fish.

Samples of macrobenthic fauna were obtained using rock-filled baskets. Baskets were placed on the river bottom in 2-4 m depths and later ($\geqq$ 90 days) collected by SCUBA divers after organism colonization. Each basket contained 14 rocks, 5 to 8 cm diameter, and covered about 200 cm^2 of bottom substrate. Previous studies indicated similar populations of benthic organisms occurred in samples from baskets and grab samples of natural substrate (Page and Neitzel, 1976a). Benthic samples were taken to the laboratory and organisms were removed from rocks by scrubbing. Organisms retained by a 0.5 mm mesh screen were preserved in 70 percent isopropyl alcohol, identified and counted. Benthic populations were expressed as number of organisms per m^2.

Duplicate stepped-oblique zooplankton tows (Page and Neitzel, 1976b) were taken from depths of 2-4 m in March and June, 1976 with a 153μ metered plankton net, 30 cm in diameter. After each 3 min tow, the net was retrieved and the sample washed into a jar. Samples were preserved in 10 percent Formalin and taken to the laboratory for species identification and enumeration.

Results

Diptera, primarily Chironomidae (midge fly), were the dominant food item, both numerically and volumetrically. Figure 1 shows percent number and percent volume of dominant food items by month and by size class of chinook fry. Since size of food organisms varied, examination of both numerical and volumetric values provided the best indication of an item's importance. Either value by itself may be misleading, especially when large (caddisfly adults) or small (zooplankton, chironomid larvae) food items are consumed. For example, chironomid larvae were numerically dominant in June yet ranked third by volume. Caddisfly adults were lowest numerically but ranked second volumetrically in June and July.

Midge fly pupae were heavily utilized and were numerically dominant in April and May when numbers of chinook fry were at peak abundance in the study area (Gray and Dauble, 1977). Midge fly larvae were important only in March and July when few fish were collected. Trichoptera adults were ingested in greatest numbers in June and July. Twenty-two percent of all chinook samples in June contained $>$ 80 percent caddisfly adults by volume. A terrestrial insect, Homoptera, family Cicadellidae, was present in large numbers in May. Zooplankters, mainly the cladoceran *Daphnia schødleri*, were consumed in all months except March. *D. schødleri* was of greatest importance in July. All other food items were usually present in trace ($<$ 1 percent) amounts only.

Ingestion of dominant food items by four size classes of chinook fry is shown in Figure 1. Midge fly pupae and larvae were most important numerically and volumetrically in the diet of fish 34-55 mm. Fish longer than 56 mm fed mainly on midge fly pupae and larvae (90 percent by number, 48 percent by volume). Caddisfly adults (2 percent by number, 39 percent by volume) were also important. Caddisfly adults were the most important food item (7 percent by number, 64 percent by volume) for chinook

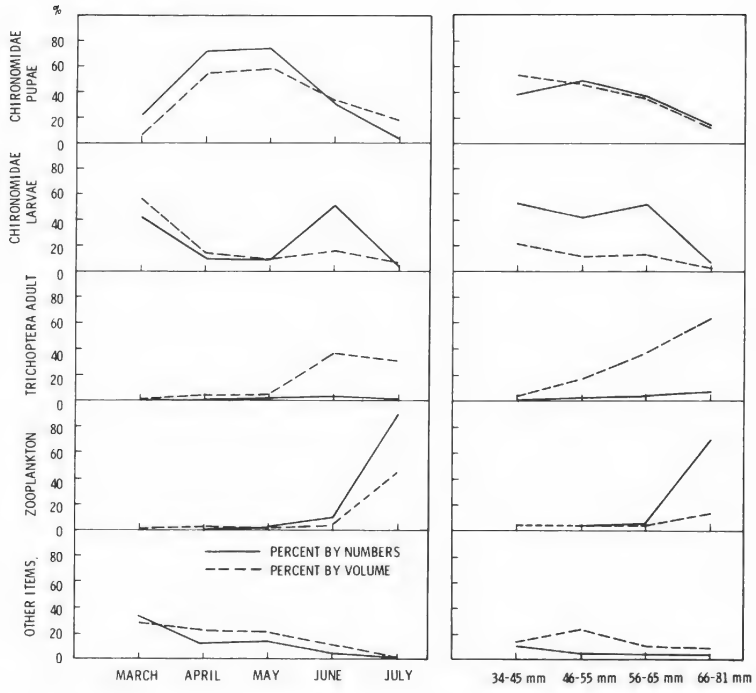

Figure 1. Relative importance of major food items by month and by size class of juvenile chinook salmon collected at Columbia River kilometer 557-613 in 1976.

fry longer than 66 mm. Crustacean zooplankton (70 percent by number, 13 percent by volume) and midge fly pupae (13 percent by number, 12 percent by volume) were also important food items for larger fish.

Table 1 summarizes the diet of all fish examined. Dipterans were clearly the dominant food item. Autochthonous food sources provided > 97 percent of the diet by number and > 90 percent by volume. These results differ from previous studies (Becker, 1973) which showed lack of zooplankton and greater consumption of Collembola by 0-age chinook fry in this section of the Columbia River.

TABLE 1. Summary of food items consumed by 0-age chinook salmon (N=260) collected in the central Columbia River, March through July, 1976.

Food Category	Percent Number	Percent Volume	Percent Occurrence
Diptera larvae	37	15	53
pupae	41	44	80
adult	2	4	21
Trichoptera larvae	<1	6	2
pupae	<1	1	2
adult	3	17	27
Terrestrial insects	2	7	22
Zooplankton	14	4	13
Arachnida	<1	<1	8
Other	<1	2	9

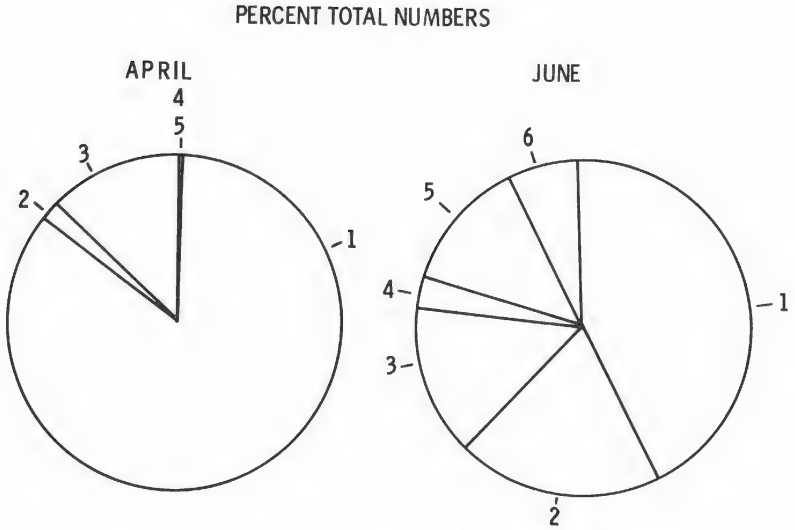

Figure 2. Relative abundance of major aquatic insect groups collected in rock-filled baskets from the benthic community in the central Columbia River, 1976. Key: 1. Chironomidae larvae; 2. Chironomidae pupae; 3. Trichoptera larvae; 4. Trichoptera pupae; 5. Simulidae larvae; 6. other insects.

Figure 2 shows the relative percentage of major aquatic insect groups collected from removable substrates placed on the river bottom. During emergence of fall chinook salmon in April, Chironomidae larvae constituted 85.2 percent and Trichoptera larvae 12.8 percent of the total benthic fauna. Although June samples were also dominated by Chironomidae larvae (46.4 percent), Trichoptera larvae (15.1 percent) and Simulidae larvae (14.4 percent) were present in increased numbers. Pupal forms of Diptera and Trichoptera were more evident in June benthic samples and supported field observations on insect emergence times.

Zooplankton samples in the mid-river drift were dominated by Copepoda, primarily *Cyclops* sp. in March and June, 1976 (Table 2). Although *Daphnia* sp. was the most abundant zooplankter present in fish guts, it was rarely found in drift samples.

TABLE 2. Mean percentages of cladoceran and copepod zooplankton sampled in midstream at Columbia River kilometer 560.

Zooplankton	March		June	
	Number/ℓ	percent	Number/ℓ	percent
Cladocera				
Daphnia spp.	—		0.4	0.7
Bosmina sp.	0.3	0.6	6.9	12.0
Chydoridae	0.7	1.5	0.9	1.6
Copepoda				
Cyclops sp.	23.5	50.8	42.3	73.8
Diaptomus sp.	21.8	47.1	6.8	11.9
Totals	46.3	100.0	57.3	100.0
Sample Volume	3.54×10^4 ℓ		3.37×10^4 ℓ	

Discussion

The availability concept in fish feeding dynamics has been discussed for young salmonids (Hoag, 1972; Carlson, 1976). Seasonal changes in diet have been attributed to seasonal changes in availability of various food items in the fish's habitat. Qualitative and quantitative changes in food supply and behavioral changes associated with fish size may be reflected in an organism's diet.

Timing of adult insect abundance and trends in benthic prey organism density were reflected in the diet of juvenile chinook salmon. Increased surface feeding by juvenile chinook salmon was noted during periods of caddisfly emergence and reflected opportunistic feeding. Although the relative large size of adult caddisflies limits the size of their predators, guts from some chinook salmon fry as small as 46 mm contained only adult caddisflies.

The frequent occurrence of midge fly larvae and pupae in young chinook salmon guts coincided with high midge numbers in benthic areas. We calculated forage ratios (Hess and Swartz, 1941), which indicated that chironomid pupae were the only benthic organisms selected in April and June (ratios, 55.4 and 1.9, respectively, when a number > 1 indicates selectivity). However, absence of larval cases in examined stomachs indicated that most midges were consumed while the highly visible pupae moved to the surface before adult eclosion. Becker (1970) considered most insect forms to have been floating, drifting or swimming in the water column when captured by chinook fry. Mundie (1971) attributed utilization of various food items of coho fry to flotation and visibility and found that chironomid adult and pupal forms were selected from the drift.

Seasonal presence of zooplankton as a major component in the diet of young chinook salmon may reflect zooplankton population fluctuations resulting from high water inundations that persisted long enough for the zooplankters to reproduce and grow. Although spatial separation of zooplankton tows could lead to discrepancies in actual availability of food items, habitat characteristics of *Daphnia schødleri* (Brooks, 1957) indicate they may be concentrated at times in shallow slack areas. Concentration of this cladoceran could result in visual discrimination from other food items and increase predator food collecting efficiency. This event could explain the presence of this cladoceran in the diet of chinook salmon fry in contrast to Becker's (1973) study. Craddock *et al.* (1976) found zooplankton were the most common item in the diet of young chinook salmon collected from July through October in the lower Columbia River. However, midstream zooplankton abundance in the lower Columbia River sometimes exceeded 4500 organisms per m^3 during the summer, whereas our samples never exceeded 400 zooplankton per m^3. Nearshore sampling of insects and zooplankton drift would be necessary before selectivity of all available food organisms could be determined.

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Palynology and Paleoecology of a Sedimentary Interbed in the Yakima Basalt (Miocene), Palouse Falls, Washington

Abstract

A thin sedimentary interbed in the middle Yakima Basalt has yielded a well-preserved middle Miocene pollen and spore flora from which the paleoecology can be inferred. The deposit, a diatomaceous tuff, lies between the two lowermost flows of the Frenchman Springs Member and has restricted outcrops in the Palouse River canyon just upstream from Palouse Falls, Washington. A total of 95 palynomorph taxa have been recognized and referred to 64 genera in 39 families. Dominant forms are *Ulmus* or *Zelkova*, *Alnus*, and *Carya*; in moderate abundance are *Equisetum*, *Typha* or *Sparganium*, *Salix*, *Nymphaea*, and *Thuja* or *Juniperus*. The assemblage is predominantly warm-temperate, although the cool-temperate genera *Larix* and *Picea* are also present. As many as three-fourths of the plants represented grow today in mesic bottomland forests or wet soils. The presence of aquatic plants, diatoms, dinoflagellates, and the alga *Pediastrum* indicate deposition took place in a shallow lake or pond.

To determine if successional changes had occurred in the flora, closely-spaced samples were taken in two measured vertical microsections. Quantitative analysis showed that aquatic and shore plants such as *Typha* or *Sparganium* generally decrease in relative abundance upward in the sections, while forest types such as *Ulmus* or *Zelkova* and *Carya* increase in numbers. This trend suggests a shallowing or infilling of the body of water, perhaps due to increased volcanic activity with associated local environmental changes.

Introduction

Volcanic sediments of the Columbia Plateau have preserved an extensive record of middle Tertiary plant communities. Both megafossil remains and microfossil algae, pollen, and spores have been studied at several localities. Among well-known Miocene floras are the Succor Creek (Graham, 1965; Taggart, 1971), the Latah (Knowlton, 1926; Berry, 1929; Fisk *et al.*, 1976), Ellensburg (Smiley, 1963), Sparta (Hoxie, 1965), the Mascall, Stinking Water, and the Blue Mountain floras (Gray, 1958; Chaney, 1959; Chaney and Axelrod, 1959). These floras generally occur in lacustrine sediments which interfinger with the basalts near the margin of the Columbia Plateau. The paleoecology of several interbeds of Miocene age has been summarized briefly by Fisk *et al.* (1977). A pollen and spore flora of an earlier age has been reported by Newman (1970) from subsurface coal and shale interbeds of the Columbia River Basalts penetrated by the Rattlesnake Hills Well No. 1, Benton County, Washington. He interpreted the age of the assemblage to be early Oligocene to middle Miocene.

Sedimentary interbeds often containing plant fragments commonly occur between individual basalt flows at various stratigraphic levels in the Columbia River Basalt Group.

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This paper describes the plant microfossil assemblage of one such interbed, a thin diatomaceous tuff in the middle Yakima Basalt near the center of the Columbia Plateau at Palouse Falls State Park. From the plants represented by the pollen and spores, we have interpreted the paleoenvironment, including both the regional climate and the local depositional environment. Abstracts of this study have previously been published (Barnett and Fisk, 1978a, 1978b).

Geographical and Geological Setting

Palouse Falls State Park is located in Sec. 31, T. 14N., R. 37E. in northeastern Franklin County, southeastern Washington (Figure 1). The interbed crops out on both sides of the Palouse River just upstream from the Palouse Falls, about 5 mi from the Snake River (Figure 2).

The regional climate is presently one of hot, dry summers and cold, moist winters, with a mean annual temperature of 9.8° C and an average annual precipitation of 36.2 cm near La Crosse, 20 mi northeast of Palouse Falls (Walters and Glancy, 1969). The modern vegetation in the study area is a sagebrush steppe community (Benson, 1957) with a dominant association of *Agropyron spicatum-Festuca idahoensis* (Franklin and

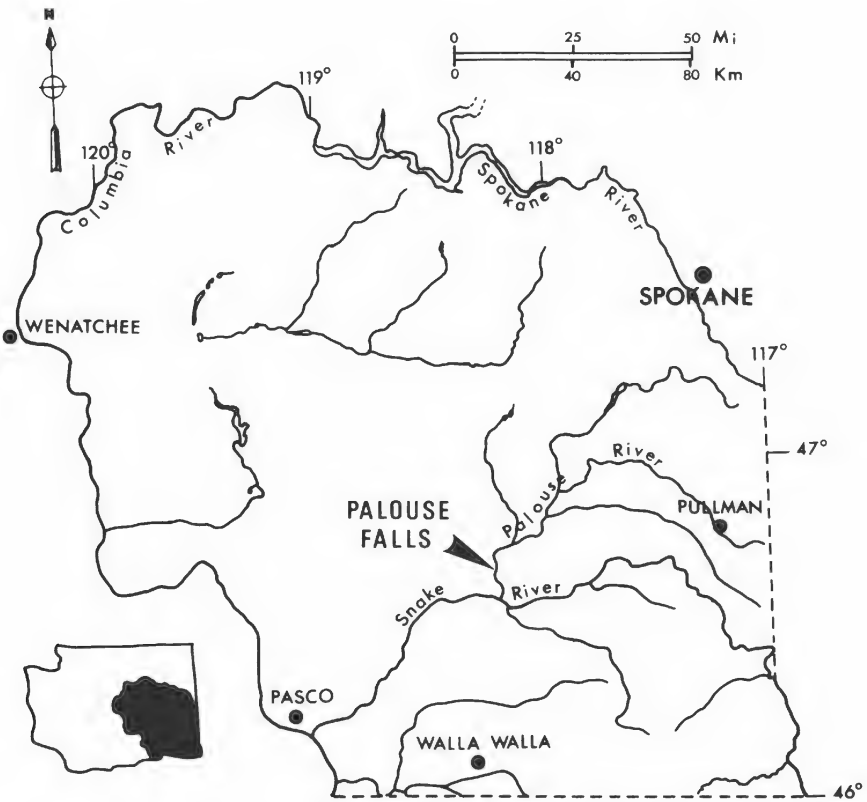

Figure 1. Map of southeastern Washington indicating the location of Palouse Falls State Park.

Figure 2. An aerial view of the Palouse Falls area, showing the topography of channeled basalt. The interbed is intermittently exposed on both sides of the river between the arrows. Photo by John Mellish.

Dyrness, 1973). The present topography of exposed and channeled basalt (Figure 2) is the result of the catastrophic Missoula Flood which swept the Columbia Plateau during the late Pleistocene (Bretz, 1959).

The Palouse Falls interbed is 15 cm to 1 m thick and is intermittently exposed from about a half mile upstream from the falls to halfway between the falls and the parking area (Figure 2). The interbed lies between the two lowermost flows of the Frenchman Springs Member of the middle Yakima Basalt (Swanson and Wright, 1976), as shown in Figures 3 and 4. The lower Frenchman Springs flow rests conformably on flows of the lower Yakima Basalt (Siems *et al.*, 1974); the contact between the lower and middle Yakima Basalts is marked by a "red top" on the flow just below the lip of the falls (Swanson and Wright, 1976). According to Siems *et al.* (1974), the middle-lower Yakima contact here and elsewhere in the Columbia River Basalt is marked by a TiO_2 discontinuity. These authors noted localities throughout the Columbia Plateau where interflow sediments, including the Vantage Sandstone, occur at this contact. The Palouse Falls interbed is one flow above the stratigraphic level of these sediments, so it is not their exact stratigraphic equivalent.

The Yakima Basalt is the uppermost and most extensive formation of the Columbia River Basalt Group (Swanson and Wright, 1976). According to Holmgren (1970), K-Ar dates for the Columbia River Basalt generally fall between 14 and 28 m.y., indicating a middle Miocene age. Everden and James (1964) gave a K-Ar date of 13.4 $\pm$ 0.4 m.y. for the Frenchman Springs Member, but Swanson (pers. comm., 1978) has suggested that an age of 14.5-15 m.y. is more likely, based on stratigraphic relationships and un-

Figure 3. Palouse Falls from the parking lot of Palouse Falls State Park. Arrow indicates stratigraphic position of the interbed. Photo by Gary Bolster.

published dates he has obtained for the Frenchman Springs flows. The flows of the Frenchman Springs Member of the middle Yakima Basalt apparently originated to the south and east of the Rattlesnake Hills-Hanford region and flowed into a slowly subsiding basin. The flows gradually thin and pinch out to the north and east (Siems *et al.*, 1974).

Methods and Materials

Sample Collection

A total of 16 samples of coal and diatomaceous tuff were collected for pollen analysis

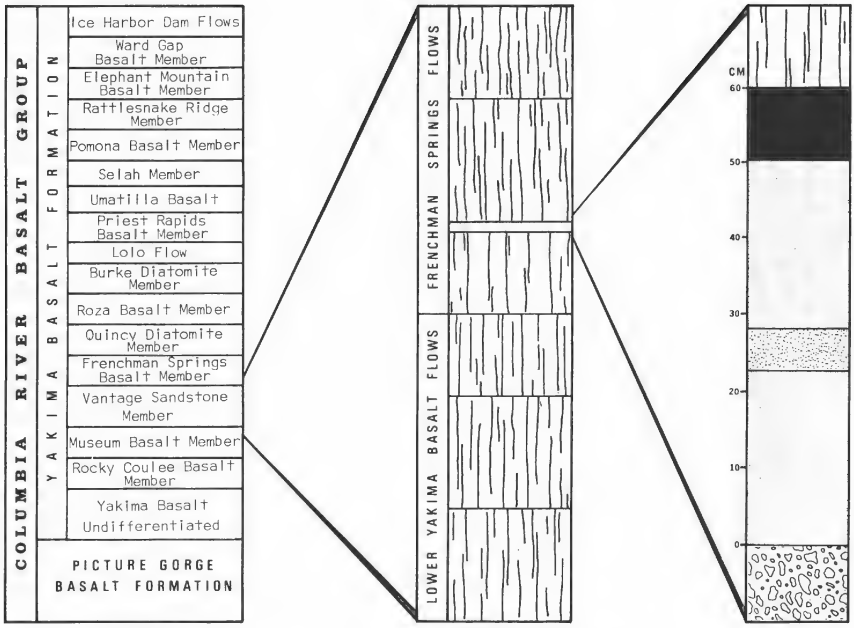

Figure 4. Stratigraphic location and lithology of the Palouse Falls interbed. See text for lithologic description. Basalt stratigraphy after Siems *et al.* (1974).

from outcrops on the south side of Palouse River. Closely-spaced samples were taken from each lithology in two measured vertical sequences or microsections through the interbed. In addition, several point samples were taken at other locations along the outcrop.

The sequence of lithologies (Figures 4 and 5) shows good correspondence between the two microsections, and parts of the sequence can be recognized at other collection sites where the interbed was not as fully exposed. Immediately overlying the lower basalt flow is an indefinite zone of breccia with pumice or scoriaceous clasts. Next occurs 8-23 cm of buff to brown tuff containing plant fragments. Above this is a layer of coarse, white to rust-colored volcanic sandstone 3-8 cm in thickness, with small slump structures or loadcasts occurring at the contact with the underlying tuff. The overlying 8-23 cm of diatomaceous tuff grades in color from cream at the base to gray near the top and contains organic-rich lamina and some thin bands of lignite. Above this tuff is a 1-10 cm thick seam of low-grade silicified coal. In some portions of the outcrop area, the coal is

Figure 5. Close-up view of the interbed illustrating the vertical change in lithology. Site of one of the microsections described in the text and diagrammatically shown in Figure 4.

overlain by a zone of brecciated basalt, whereas in other areas the basalt is not brecciated.

Sample Preparation

The resistant outer wall or exine of the pollen grain allows rather rigorous chemical treatment in breaking down the rock matrix and isolating the pollen and spores. The maceration techniques outlined below are standard for many kinds of palynological samples. More detailed procedures have been described by Brown (1960), Gray (1965), Barss and Williams (1973), and Doher (1973).

Chemical demineralization was accomplished with dilute hydrochloric acid to remove the carbonates, followed by hydrofluroic acid to remove the silicates. Carbonaceous material was oxidized with Schulze solution (a 2:1 mixture of nitric acid with aqueous potassium chlorate). The remaining mineral residue was separated from the organic fraction containing the pollen and spores by differential flotation in a zinc bromide solution with a specific gravity of 1.96. Samples full of organic debris were acetolyzed with acetic anhydride and concentrated sulfuric acid and oxidized with sodium hypochlorite ("Chlorox"). The organic residue was then stained with safranin and microscope slides were prepared using the coverslip mounting technique described by Schopf (1964). The mounting medium was hydroxyethylcellulose and the coverslip was cemented to the slide with Harleco synthetic resin.

Analysis and Identification

The microfossils found on the slides were photographed on Kodak Panatomic-X film using a Zeiss photomicroscope. Each palynomorph type was morphologically coded ac-

cording to a system similar to that proposed by Tschudy (1957). To identify the palynomorphs, comparison was made with descriptions and photomicrographs of fossil pollen and spores in the literature (e.g., Gray, 1958; Martin and Rouse, 1966; Hopkins, 1969; Snead, 1969; Piel, 1971; Jansonius and Hills, 1976). Also helpful were modern reference slides and descriptions of modern pollen given in the standard text by Wodehouse (1935) and the illustrated keys of Kapp (1969) and McAndrews *et al.* (1973). All pollen-bearing samples were analyzed quantitatively for the relative abundance of each palynomorph type. A total of 500 palynomorphs was counted per sample, including fungal spores, acritarchs, and algae.

In the palynological literature, taxonomy of Tertiary pollen and spores is a rather chaotic array of two basic approaches (see discussion by Taggart, 1971, pp. 84-92). One approach is to use form- or organ-genera based solely on morphology. This system is commonly used for extinct Paleozoic and Mesozoic forms, which bear little, if any, resemblance to modern spores. The alternate approach commonly used in Pliocene and Pleistocene studies is to assign all fossil palynomorphs to modern taxa. Since the Tertiary represents a period of transition from older extinct to modern forms, both systems of taxonomy have been used. For paleoecological purposes, it is essential to know the modern botanical affinity of fossil pollen and spores; hence, we have assigned the Palouse Falls palynomorphs to modern taxa where the affinities are fairly certain. Otherwise, a form- or organ-genus was used, or if unidentified, the type was designated by its morphological code number, e.g., Tricolpate-2.

Results and Discussion

Palynomorph Assemblage

Of the sixteen samples analyzed, ten contained abundant and well-preserved microfossils. Samples of coal and the immediately underlying tuff were barren.

A total of 95 morphotypes has been recognized and assigned to 64 genera in 39 families (Table 1). These palynomorphs are distributed in the major groups as follows: 3 percent algae, 1 percent fungi, 7 percent ferns, 14 percent gymnosperms, and 39 percent angiosperms; 28 percent remain unidentified. Dominant taxa are *Ulmus* or *Zelkova*, *Alnus*, and *Carya*, with *Ulmus* or *Zelkova* composing over 50 percent of some samples. In moderate abundance are *Equisetum*, *Typha* or *Sparganium*, *Salix*, *Nymphaea*, and *Thuja*- or *Juniperus*-type pollen. Other typical Miocene genera found include *Abies*, *Acer*, *Liquidambar*, *Pterocarya*, *Juglans*, *Betula*, *Corylus*, *Quercus*, *Fagus*, *Nyssa*, and *Tilia*.

Caution must be used in interpreting quantitative information from pollen samples since there is not a simple correspondence between the abundance of a specific pollen in a sample and the importance of its parent plant in the region. A number of factors influence the total amounts of pollen in a palynological preparation (Gray, 1958). Most obvious are those which are related to the pollen production of the parent plant—whether it is wind-pollinated and producing huge amounts of airborne pollen, or whether it is insect-pollinated, producing relatively few grains. Also important is dispersion; some pollen grains such as *Pinus* are adapted for long-distance transport, whereas others, especially insect-pollinated species, are distributed only locally. In addition, although the pollen and spore exine is fairly resistant to destruction, differential preservation in the sediments, as well as differential destruction during laboratory treatment, does occur. For example, grains of *Ulmus* or *Zelkova* are known to be virtually indestructible

TABLE 1. Systematic list of microfossils found in Palouse Falls sediments.

CHLOROPHYTA	
HYDRODICTYACEAE	
Pediastrum sp.	
ZYGNEMATACEAE	
Mougeotia sp.	
Schizosporis sp.	
INCERTAE SEDIS	
ACRITARCHA	
ACANTHOMORPHITAE	
Baltisphaeridium sp.	
Micrhystridium sp. type 1	
Micrhystridium sp. type 2	
Micrhystridium sp. type 3	
EUMYCOPHYTA	
Diporisporites sp.	
PTERIDOPHYTA	
LYCOPSIDA	
LYCOPODIACEAE	
Lycopodium sp.	Club moss
SELAGINELLACEAE	
Selaginella sp.	Spike moss
SPHENOPSIDA	
EQUISETACEAE	
Equisetum sp.	Horsetail ; Scouring rush
FILICOPSIDA	
POLYPODIACEAE	Common fern family
Laevigatosporites albertensis Rouse	
Laevigatosporites ovatus Wilson and Webster	
Verrucatosporites sp.	
SALVINIACEAE	
Azolla sp.	Water fern
INCERTAE SEDIS	
Concavisporites jurienensis Balme	
Deltoidospora sp.	
Triplanosporites sp.	
INCERTAE SEDIS	
Inaperturate-3	
Trilete-2	
Trilete-3	
Trilete-9	
Trilete-12	
Trilete-14	
SPERMATOPHYTA	
GYMNOSPERMAE	
CUPRESSACEAE	Cypress family
Thuja or **Juniperus** type	
PINACEAE	
Abies sp.	Fir
Cedrus perialata Martin and Rouse	Cedar
?Larix sp.	Larch ; Tamarack
Picea sp.	Spruce
Pinus sp. type 1	Pine
Pinus sp. type 2	Pine
Tsuga sp.	Hemlock

TABLE 1. Continued

PODOCARPACEAE	
Podocarpus sp.	Podocarpus
TAXODIACEAE	
Taxodium hiatipites Wodehouse	Swamp-cypress
TAXODIACEAE — CUPRESSACEAE — TAXACEAE, undivided	
INCERTAE SEDIS	
Cycadopites sp. type 1	
Cycadopites sp. type 2	
ANGIOSPERMAE	
MONOCOTYLEDONAE	
GRAMINEAE	Grass family
Graminidites sp.	
?PANDANACEAE	Screw pine family
Pandanidites texus (Simpson) Elsik	
POTAMOGETONACEAE	
Potamogeton sp.	Pondweed
TYPHACEAE or SPARGANIACEAE	
Typha sp. or **Sparganium** sp.	Cat-tail or Bur-weed
INCERTAE SEDIS	
Liliacidites sp.	
DICOTYLEDONAE	
ACERACEAE	
Acer sp.	Maple; Box elder
AQUIFOLIACEAE	
Ilex sp.	Holly
BETULACEAE	
Alnus sp.	Alder
Betula sp.	Birch
Carpinus ancipites Wodehouse	Hornbeam
Corylus sp.	Hazel
Ostrya oregoniana Chaney	Hop-hornbeam; Ironwood
CHENOPODIACEAE	Goosefoot family
cf. Sarcobatus sp.	
CORIARIACEAE	
Coriaripites sp.	
ERICACEAE	
Vaccinium sp.	Cranberry; Blueberry
FAGACEAE	
Fagus verus (Raatz) Martin and Rouse	Beech
Quercus sp.	Oak
HAMAMELIDACEAE	
Liquidambar sp.	Sweetgum
JUGLANDACEAE	
Carya spp.	Hickory; Pecan
Juglans sp.	Walnut; Butternut
Pterocarya sp.	Wingnut
LABIATAE	Mint family

TABLE 1. Continued

MALVACEAE	Mallow family
Malvacipollis diversus Harris	
Malvacearumpollis sp.	
MORACEAE	
Morus sp.	Mulberry
NYMPHACEAE	
Nymphaea polymorpha Lyubomirova	Water lily
NYSSACEAE	
Nyssa sp.	Sourgum; Tupelo
OLEACEAE	
Fraxinus sp.	Ash
ONAGRACEAE	
Jussiaea sp.	Primrose-willow
PLATANACEAE	
Platanus sp.	Plane-tree, Sycamore
POLYGONACEAE	
?Polygonum sp.	Knotweed
SALICACEAE	
Populus sp.	Poplar
Salix discoloripites Wodehouse	Willow
THEACEAE	
Gordonia sp.	
TILIACEAE	
Tilia sp.	Basswood
ULMACEAE	
Celtis sp.	Hackberry
Ulmus sp. or **Zelkova** sp.	Elm
INCERTAE SEDIS	
Inaperturate-13	
Inaperturate-14	
Inaperturate-19	
Inaperturate-20	
Inaperturate-22	
Stephanocolpate-1	
Stephanocolpate-3	
Stephanocolpate-7	
Tricolpate-6	
Tricolpate-8	
Tricolpate-9	
Tricolpate-15	
Tricolpate-16	
Tricolpate-22	
Tricolpate-23	
Tricolpate-26	
Tricolpate-27	
Tricolpate-29	
Tricolporate-3	
Triporate-2	
Triporate-10	
TOTAL:	39 Families
	64 genera

(Gray, 1958), which may partially account for their abundance in some samples which are otherwise poor in pollen.

In addition to the pollen and spore assemblage, several algal types occurred in most of the samples. The freshwater colonial alga *Pediastrum* is a well-known fossil form, first occurring in the early Cretaceous (Evitt, 1969). Another alga which we have identified as *Mougeotia* resembles types traditionally designated as *Tetraporina*, a form-genus reported from Paleozoic through Tertiary sediments (Scott *et al.*, 1960). *Tetraporina* has been identified with aplanospores of the modern genus *Tetraedron* by various workers (Scott *et al.* 1960). Recently, van Geel (1976) has pointed out that this form most closely resembles the zygospores of the modern genus *Mougeotia*, rather than *Tetraedron.* In addition, acritarchs belonging to the genera *Micrhystridium* and *Baltisphaeridium* occur in some abundance. The botanical affinities of the acritarchs are uncertain, though some have been referred to the dinoflagellates or to various life stages of unicellular and higher organisms (Evitt, 1969).

Paleoecology

The ecological habitat, climatic range, and geographical distribution for each taxon represented in the Palouse Falls sediments are given in Table 2. The flora represented is predominantly warm temperate, although a few typically cool temperate genera also occur, as shown in Figure 6. Several genera such as *Pterocarya*, *Liquidambar*, *Jussiaea*, *Juglans*, *Gordonia*, *Taxodium*, *Podocarpus*, and *Azolla* variously range from tropical through warm temperate regions, but do not normally extend into cool temperate latitudes. On the other hand, *Larix*, *Picea*, and *Abies* are typically cool temperate to boreal in distribution. None of the genera are restricted to tropical-subtropical or boreal zones. The association of plants found most closely resembles the Eastern Deciduous Forest and Coastal Plain provinces of Gleason and Cronquist (1964). Nearly all the taxa of the paleoflora are now foreign to the region, and the community represented stands out in marked contrast to the present day sagebrush-grass community in the Palouse Falls area.

Figure 7 presents an overall picture of the environmental requirements of the taxa represented by the palynomorphs. Nearly 75 percent of the plants grow in mesic bottomland, slope forests, or wet soil, with about 50 percent being restricted to, or most often found in, these habitats. Typical trees and shrubs of this group are *Alnus*, *Carpinus*, *Carya*, *Corylus*, *Fraxinus*, *Juglans*, *Liquidambar*, *Platanus*, *Salix*, *Tilia*, and *Ulmus* or *Zelkova.* Indicators of dry slope, montane, or boreal forests include *Abies*, *Picea*, and *Larix.* None of the plants are today found exclusively in dry soil, steppe, or desert environments. Several taxa, however, presently live only in slow-moving streams or in the shallow waters of ponds and lakes. These include the phytoplankton *Pediastrum*, *Micrhystridium*, and *Baltisphaeridium*, along with the aquatic macrophytes *Azolla*, *Potamogeton*, and *Nymphaea.* In addition, *Typha*, *Sparganium*, and *Jussiaea* typically grow in shallow water, marshes, or wet soil. A more specific paleoenvironmental indicator is the alga *Mougeotia* of the family Zygnemataceae. According to van Geel (1976), the formation and germination of zygospores of this family occur only in stagnant, mesotrophic freshwater, less than 0.5 m in depth.

Microstratigraphic Distribution

The relative abundance of the most common taxa (those which comprise 2 percent or

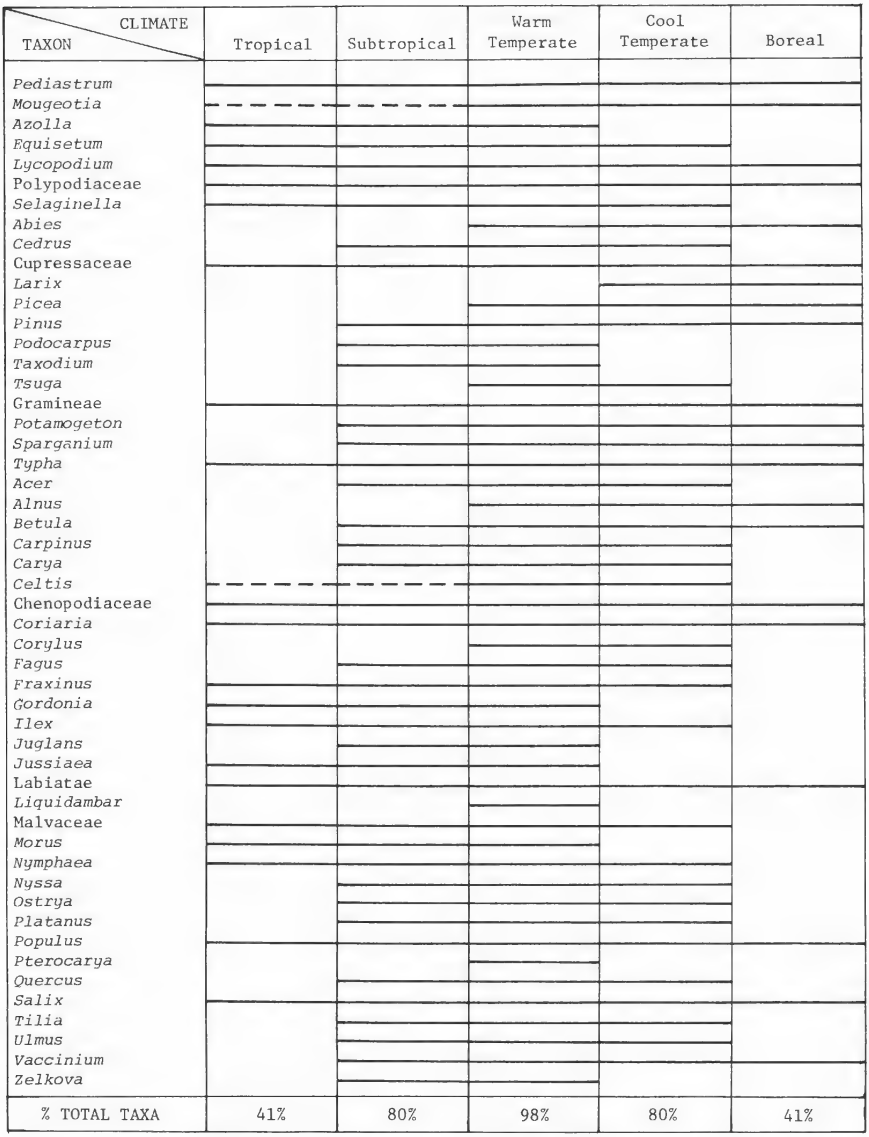

Figure 6. Climatic ranges of the modern taxa represented by the Palouse Falls palynomorphs. Solid lines indicate the known range of the taxon; dashed lines indicate that the range is uncertain.

more of at least one sample) are graphed in Figure 8. The data show a trend which seems to indicate a successional change in the flora. Aquatic and shore plants such as *Typha* or *Sparganium*, *Nymphaea*, and *Salix*, along with *Equisetum*, decrease upward in the section. On the other hand, the forest genera *Alnus*, *Carya*, *Pterocarya*, *Ulmus* or

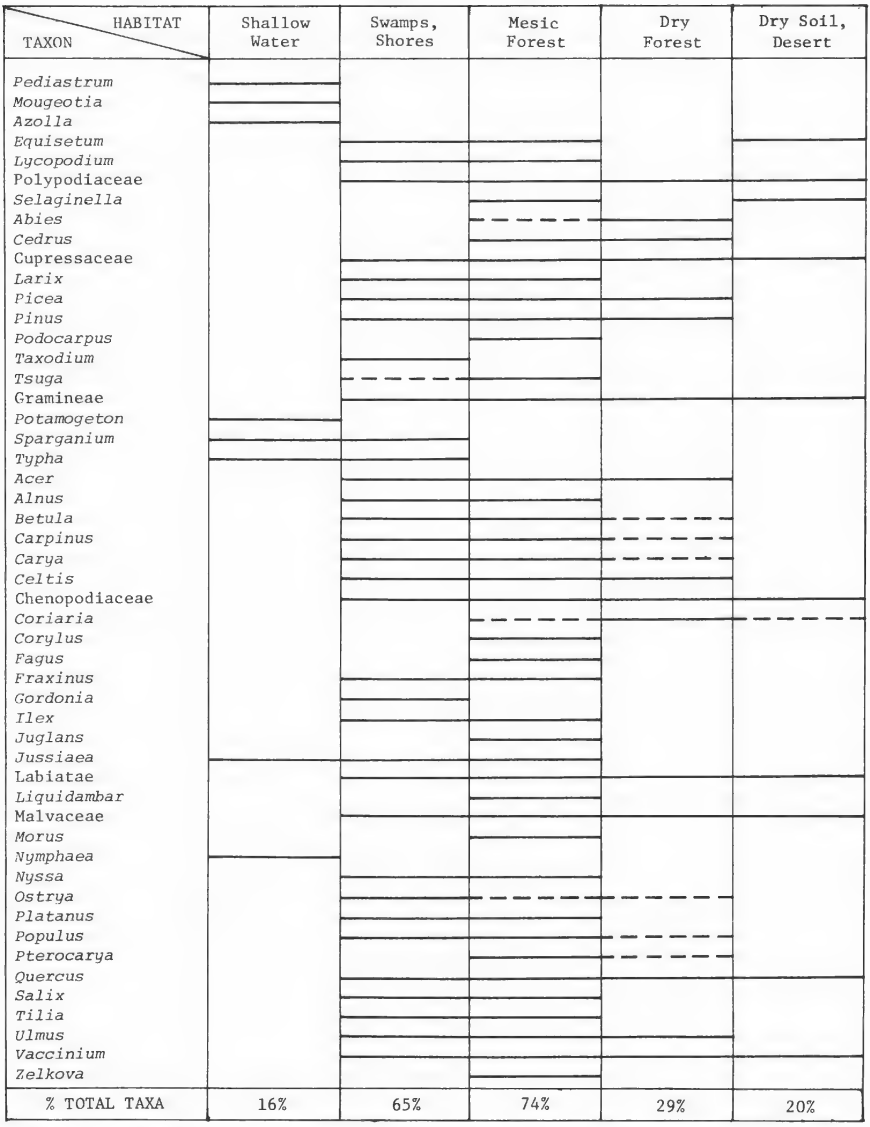

Figure 7. Generalized ecological habitats of the modern taxa represented by the Palouse Falls palynomorphs. Solid lines indicate known habitats of the taxa; dashed lines indicate that the habitat is uncertain.

Zelkova, and *Thuja* or *Juniperus* generally increase in relative abundance. The distribution of the ecological indicators is shown in Figure 9. Although a successional change is not well marked, the upward trend again appears to show a slight decrease in marsh and shore plants and an increase in mesic forest elements.

TABLE 2. Ecological characteristics and distribution of extant taxa represented by the Palouse Falls microfossils. Modified after Pierce (1961), Rouse (1962), Smiley (1966), Hopkins (1969) and Fisk (1976), with additions from Lawrence (1951), Gray (1958), Willis (1973), and Rachele (1976).

TAXON	HABITAT	CLIMATE	GEOGRAPHIC RANGE
ALGAE			
Pediastrum	fresh-water lakes, ponds, and slow-moving streams	tropical to boreal	cosmopolitan
Zygnemataceae	shallow, stagnant, mesotrophic fresh-water	(tropical, subtropical?) temperate to boreal	Northern Hemisphere; Kerguelen Islands
PTERIDOPHYTES			
Azolla	aquatic in quiet lakes and ponds	tropical to warm temperate	all continents except Europe
Equisetum	swamps and moist woods to dry soils	tropical to cool temperate	cosmopolitan except Australasia
Lycopodium	moist areas, sometimes epiphytic	tropical to boreal	cosmopolitan
Selaginella	mostly damp areas, a few xerophytic	tropical to cool temperate	cosmopolitan
Polypodiaceae	rain forest to deserts	tropical to boreal	cosmopolitan
GYMNOSPERMS			
Abies	highlands and mountainous regions	warm temperate to boreal	Northern Hemisphere, south to Guatamala and northern Africa
Cedrus	dense mesic to dry forests	subtropical to cool temperate	Mediterranean region, northern Africa, western Himalayas
Cupressaceae	variable	tropical to boreal	cosmopolitan
Larix	marshes and wet woodlands	cool temperate to boreal	Northern Hemisphere
Picea	swamps to well-drained upland slopes	warm temperate to boreal	Northern Hemisphere
Pinus	swamps to dry, rocky highlands	subtropical to boreal	Northern Hemisphere
Podocarpus	moist woodlands	subtropical to warm temperate	Southern Hemisphere, north to Mexico, southern Japan, and central China
Taxodium	swamps, streambanks, and flood plains	subtropical to warm temperate	southeastern U.S. and Mexico
Tsuga	moist woodlands	warm to cool temperate	North America, Himalayas to Japan
ANGIOSPERMS			
MONOCOTYLEDONS			
Gramineae	variable	tropical to boreal	cosmopolitan

TABLE 2. Continued

Potamogeton	aquatic in fresh-water lakes, ponds, and streams	subtropical to boreal	mainly Northern Hemisphere
Sparganium	aquatic in ponds and lakes; marshes	subtropical to boreal	cosmopolitan
Typha	marshes; shallow water of ponds and lakes	tropical to boreal	cosmopolitan
DICOTYLEDONS			
Acer	variable, but often moist uplands and mountainous regions	subtropical to cool temperate	Northern Hemisphere
Alnus	swamps, streambanks, wet slopes	warm temperate to boreal	Northern Hemisphere, south to Central America and Andes Mts.
Betula	bogs and swamps to moist uplands	subtropical to boreal	Northern Hemisphere
Carpinus	coastal swamps to moist uplands	subtropical to cool temperate	Northern Hemisphere
Carya	variable; often moist woodlands and streambanks	subtropical to cool temperate	eastern North America, China, southeast Asia
Celtis	wet lowlands to rocky hills and barrens	(tropical, subtropical?) warm to cool temperate	Northern Hemisphere, South Africa
Chenopodiaceae	variable; often dry and alkaline soil	tropical to boreal	cosmopolitan
Coriaria	humid thickets and stream margins, dry woods and rocky places	tropical to boreal	western Mediterranean, Asia, Australasia, Central America and western South America
Corylus	thickets and woodlands	warm to cool temperate	Northern Hemisphere
Fagus	mesic forests	subtropical to cool temperate	Northern Hemisphere
Fraxinus	damp woods, swamps	tropical to cool temperate	Northern Hemisphere, Cuba and Java
Gordonia	non-alluvial swamps, often in acid soil	tropical to warm temperate	southeast Asia, southeastern North America
Ilex	bogs, low moist areas	tropical to cool temperate	cosmopolitan
Juglans	moist woods, river terraces	subtropical to warm temperate	southeastern U.S., southeastern Europe to eastern Asia; Central America and Andes Mts.
Jussiaea	wet soil; aquatic in shallow water	tropical to warm temperate	southern U.S. south to Argentina
Labiatae	variable; marshes to deserts	tropical to boreal	cosmopolitan

TABLE 2. Continued

Liquidambar	moist or wet woods	subtropical to warm temperate	Northern Hemisphere
Malvaceae	variable	tropical to cool temperate	cosmopolitan
Morus	moist woods	tropical to warm temperate	nearly cosmopolitan
Nymphaea	aquatic in ponds, lakes, and slow-moving streams	tropical to cool temperate	Northern Hemisphere
Nyssa	swamps and lakeshores to moist, low woods	subtropical to cool temperate	eastern U.S. and Asia
Ostrya	coastal swamps to upland woodlands	subtropical to cool temperate	Northern Hemisphere
Platanus	lowlands, streambanks and lake shores	subtropical to cool temperate	Northern Hemisphere
Populus	dry or usually moist soil: watercourses	tropical to boreal	Northern Hemisphere, eastern Africa
Pterocarya	light woods and wet soils	warm temperate	Caucasus Mts. to China and Japan
Quercus	variable; dry to mesic forests	subtropical to cool temperate	Northern Hemisphere, mountains of the tropics
Salix	moist thickets, swamps, streambanks	tropical to boreal	cosmopolitan
Tilia	moist slopes, streambanks, floodplains	subtropical to cool temperate	Northern Hemisphere
Ulmus	river valleys, moist woodlands to dry uplands	subtropical to cool temperate	Northern Hemisphere
Vaccinium	variable; swamps and bogs to dry sandy woods	subtropical to boreal	Northern Hemisphere, tropical mountains
Zelkova	moist woodlands	subtropical to warm temperate	eastern Mediterranean, Caucasus Mts. east to central China and Japan

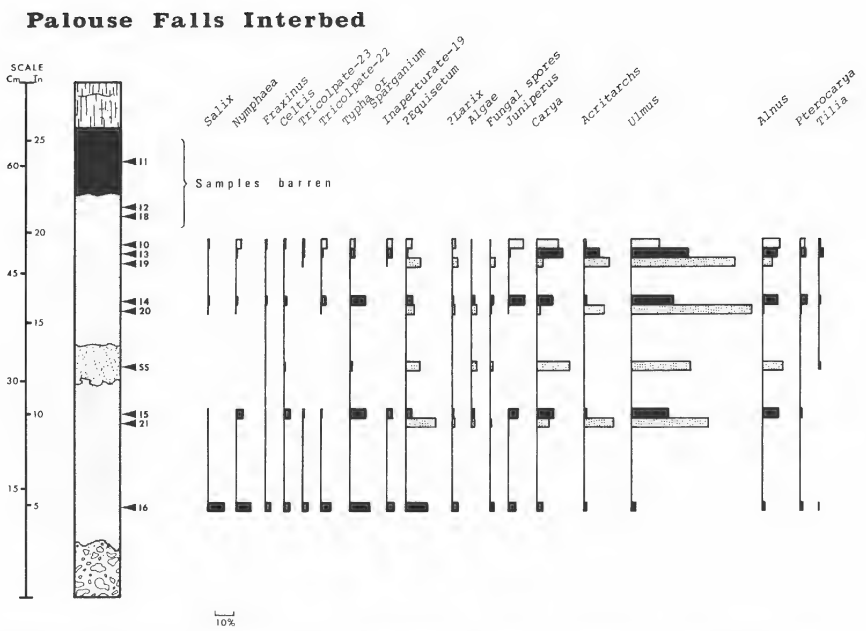

Figure 8. Relative abundances of the most abundant groups (taxa which comprise 2 percent or more of at least one sample). The distributions of the taxa in the two microsections are distinguished by solid and stippled bars. Sample 10 is from a third location. The taxa are arranged from left to right in order of decreasing mean depth, which marks the center of distribution of the taxa.

Comparisons with Other Miocene Palynofloras

The warm temperate climate indicated by the Palouse Falls palynoflora is typical of other middle Miocene floras of the Northern Hemisphere, and particularly those of the Columbia Plateau. In a study of three palynofloras from middle-upper Miocene diatomaceous tuffs overlying the Columbia River basalt in eastern Oregon, Gray (1958) concluded that the microfossil as well as megafossil record indicated that the "Miocene vegetation of Oregon was composed predominantly of deciduous trees and shrubs now living in summer-wet forests of temperate middle latitudes of eastern America and Asia." For the middle Miocene Succor Creek palynoflora of southeastern Oregon and adjacent Idaho, Taggart (1971) reported a succession of plant communities: first a lowland, probably cool temperate deciduous forest with an adjacent montane coniferous forest, followed by swamp and marsh communities corresponding to an extensive impoundment of water, and finally a "depauperate riparian forest" in a predominantly xeric region. Smiley (1963) described a somewhat similar vegetational succession from a swamp cypress forest through a deciduous hardwood forest to a semi-arid forest for the late Miocene-early Pliocene Ellensburg Formation of central Washington. The Sparta palynoflora (Hoxie, 1965) of the southern foothills of the Wallowa Mountains is also quite similar in overall composition to the Palouse Falls palynoflora. It also comes from a thin interbed but occurs in the older Picture Gorge Basalt. Hoxie interpreted the age to be middle Miocene and assumed a mesic deciduous forest in a small upland valley with a coniferous

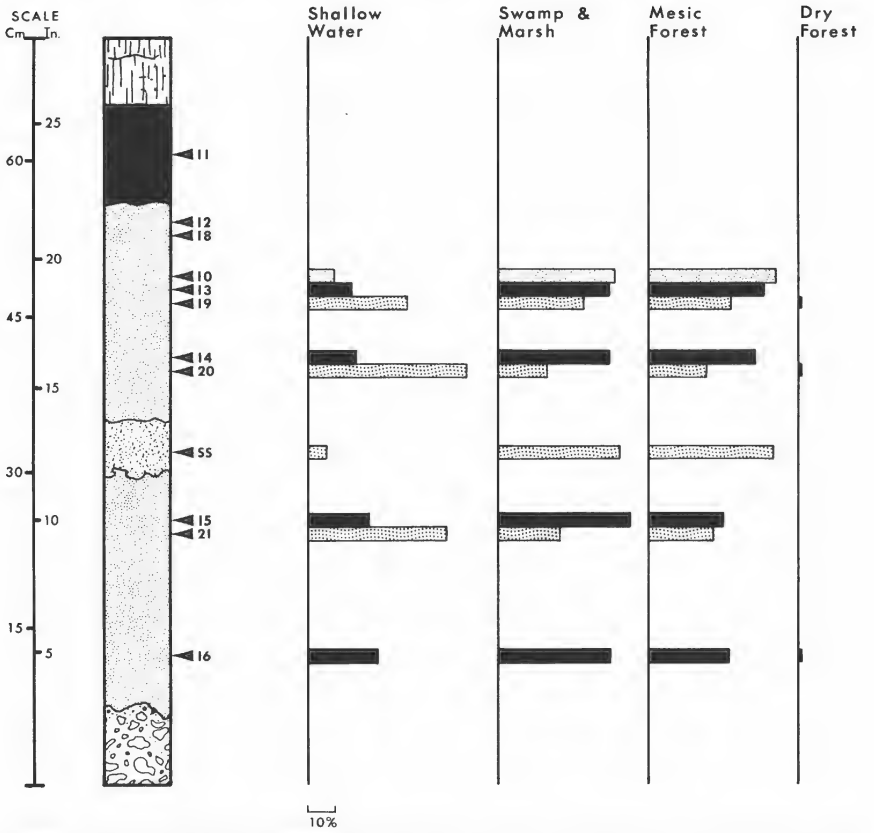

Figure 9. The normalized percentages of the indicator species (those which are restricted to one or two zones in Figure 7).

forest on nearby hills or mountains. Summarizing the Neogene climate for the Pacific Northwest, Leopold (1969) noted that the pollen evidence indicates a subtropical to warm temperate climate in the Miocene and a temperate climate in the Pliocene.

Conclusion

The Palouse Falls palynoflora reflects reasonably well the regional climatic conditions as evidenced by related floras of the Columbia Plateau. The presence of planktonic forms, aquatic macrophytes, and marsh plants indicates that deposition of the sediments took place in a body of water, probably a pond or shallow lake. This interpretation is supported by the presence of abundant diatoms. The general decrease in aquatic plants and increase in forest elements upward in the section suggest a shallowing or infilling of the pond or lake, perhaps due to increased volcanic activity and erosion of ash from the surrounding region. Supporting this view is the presence of thin bands of lignite near the top

of the section, with a 1-10 cm coal layer just underlying the capping basalt.

The presence of well-preserved palynomorphs in a small, stratigraphically isolated interbed suggests that valuable paleoecological and possibly biostratigraphical information can be obtained from similar interbeds scattered throughout the Columbia Plateau at various stratigraphic horizons. Swanson and Wright (1976) have remarked that the zone of weathering and "soil formation" which developed before the eruption of the flows of the Frenchman Springs Member is important in working out the stratigraphy. Similarly, pollen- and spore-bearing interbeds may have potential in establishing a biostratigraphic framework for recognizing and correlating individual flows in the sequence (Fisk *et al.*, 1977).

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Mites Found in the Fur of a Small Sample of Heteromyid Rodents from Oregon

Abstract

The most abundant external parasitic mites on *Dipodomys ordii* from Oregon were *Geomylichus texensis*, *Androlaelaps fahrenholzi*, and *Hirstionyssus incomptis*; on *Perognathus parvus* they were *A. fahrenholzi* and *Geomylichus* n. sp. New host records during this study were *Haemogamasus reidi* and *H. onychomydis* on *D. ordii* and *H. onychomydis* and *Geomylichus* n. sp. on *P. parvus*. Parasites not previously reported from Oregon are *Geomylichus texensis*, *Hirstionyssus incomptis*, *H. hilli*, *Haemogamasus onychomydis*, *Ischyropoda armatus*, and *I. furmani*.

Introduction

The present paper is part of our continuing studies on parasitic mites of Oregon mammals, and concerns hosts for which there is relatively little parasite information available. Mites were collected by brushing and picking them off the fur. More smaller mites would undoubtedly have been found by a more exacting examination of the fur with the aid of a dissecting microscope.

Results and Discussion

Four species of heteromyid rodents were examined for mites during the present study, one chisel-toothed kangaroo rat, *Dipodomys microps* (which had no mites), 36 Ord's kangaroo rats, *D. ordii*, one dark kangaroo mouse, *Microdipodops megacephalus*, and 34 Great Basin pocket mice, *Perognathus parvus*.

Dipodomys ordii. Twenty-one of the 36 kangaroo rats examined had mites (Table 1). The most abundant mites were *Geomylichus texensis*, *Androlaelaps fahrenholzi*, and *Hirstionyssus incomptis*. There are several reports of the latter two species on this host, whereas *G. texensis* was recently described from this host and from *D. merriami* from Texas and from *Perognathus penicillatus* from Arizona (Fain *et al.*, 1978). *Haemogamasus reidi* and *H. onychomydis* are new host records.

Perognathus parvus. Fifteen of the 34 pocket mice examined had mites (other than chiggers) (Table 1). The most abundant mites were *Androlaelaps fahrenholzi*, *Proctolaelaps* sp., and *Geomylichus* n. sp. The only parasitic species not previously reported from

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P. parvus are *Haemogamasus onychomydis* and *Geomylichus* n. sp. (currently being descibed by Fain and Whitaker).

TABLE 1. Mites found in the fur of heteromyid rodents from Oregon.

	Dipodomys ordii (n=36)				**Perognathus parvus (n=34)**			
	Hosts Infested		Parasites		Hosts Infested		Parasites	
	No.	%	No.	Av./host	No.	%	No.	Av./host
LAELAPIDAE								
Androlaelaps fahrenholzi	10	27.8	36	1.0	11	32.4	28	0.8
Hirstionyssus incomptis	9	25.0	21	0.6				
Ischyropoda armatus	4	11.1	7	0.2	4	11.8	4	0.1
Ischyropoda furmani	1	2.8	4	0.1				
Hirstionyssus triacanthis	1	2.8	2	0.1				
Haemogamasus reidi	1	2.8	2	0.1				
Hirstionyssus utahensis	1	2.8	2	0.1				
Haemogamasus onychomydis	2	5.6	2	0.1	1	2.9	1	0.03
Hirstionyssus hilli	1	2.8	1	0.03	4	11.8	5	0.1
LISTROPHORIDAE								
Geomylichus texensis	8	22.2	69	1.9				
Geomylichus n. sp.					3	8.8	9	0.3
Other Mites								
Kleemania sp.	1	2.8	8	0.2	3	8.8	4	0.1
Macrocheles sp.	1	2.8	2	0.1				
Proctolaelaps sp.	2	5.6	2	0.1	1	2.9	12	0.4
Euryparasitus sp.	1	2.8	2	0.1				
Bakerdania sp.					1	2.9	6	0.2

Microdipodops megacephalus. On the one individual examined, three immature listrophorid mites were found. Since the only previous mite reported from this species of which we are aware (Whitaker and Wilson, 1974; Fain and Hyland, 1974) is *Ischyropoda armatus*, extra effort should be made to examine this species for listrophorids and for other external parasites.

Mites not previously reported from Oregon are *Geomylichus texensis*, *Hirstionyssus incomptis*, *H. hilli*, *Haemogamasus onychomydis*, *Ischyropoda armatus*, and *I. furmani.*

Kleemania, *Proctolaelaps*, *Euryparasitus*, and *Bakerdania* are apparently not parasitic, although they are found fairly often on small mammals. *Macrocheles* is probably phoretic.

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Aerial Survey of Pacific Harbor Seals in the Southeastern Bering Sea

Abstract

Between June 1975 and June 1977, five aerial surveys were conducted along the eastern Aleutian Islands and throughout Bristol Bay to study the distribution and abundance of the harbor seal (*Phoca vitulina richardsi*) during the breeding season. The number of group sightings and the total number of seals observed varied significantly with the tide height ($P<0.01$). Fifty-seven percent more seals were observed on a low tide than in the same area surveyed near high tide. Three locations—Port Moller, Port Heiden, and Cinder River along the north side of the Alaska Peninsula—accounted for 78 percent of the study area population count, and for approximately 8.5 percent of the entire Alaska population estimate. A minimum abundance for the study area is estimated at 29,000 animals.

Introduction

The Pacific land breeding harbor seal (*Phoca vitulina richardsi*) ranges along the west coast of North America from Baja California to the southern Bering Sea (Rice, 1977). These animals are primarily found in coastal waters but are occasionally seen up to 50 mi offshore (Calkins *et al.*, 1975). They characteristically haul out on offshore rocks swept at high tide, sand beaches, and sandbars exposed at low tide. Harbor seals are abundant throughout southeastern Alaska, the Gulf of Alaska, Aleutian Islands, Bristol Bay, and north to the Pribilof Islands (Alaska Dept. Fish and Game, 1973). The population abundance for the state of Alaska is estimated at 270,000 animals (Brooks, 1979).

Census data for harbor seals in the Bering Sea are incomplete. Opportunistic recordings were made by Mathisen and Lopp (1963) in Port Heiden, Port Moller, and Izembek Bay during their sea lion survey, but no full counts were taken. Census and behavioral observations of harbor seals at Otter Island (near the Pribilof Islands) and in Nanvak Bay (northwest Bristol Bay) were made during the summers of 1975 and 1976, results of which are not yet available (F. H. Fay, pers. comm.). Systematic surveys of the Bristol Bay coast for harbor seals have never been performed. The objectives of our study were to identify important hauling out sites and to estimate the relative abundance and distribution of the harbor seal along the north side of the Alaska Peninsula and eastern Aleutian Islands during the height of the breeding season (June-August).

Study Area and Methods

This study was conducted along the north coast of Bristol Bay from Cape Pierce to

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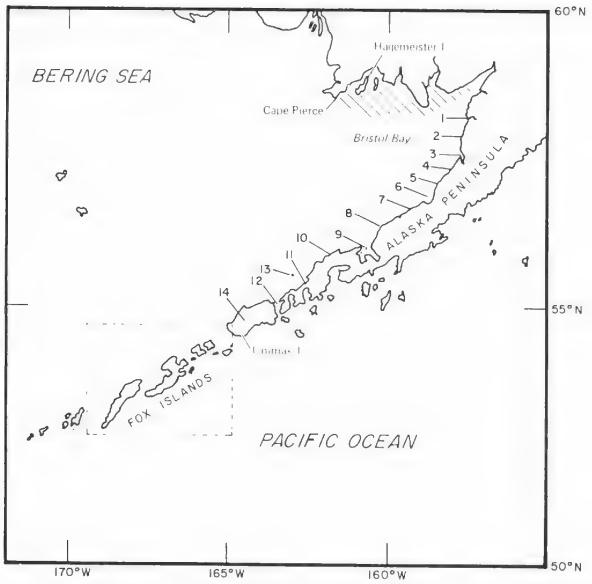

Figure 1. Haul out areas for harbor seals in the Bering Sea: north coast of Bristol Bay and the north side of the Alaska Peninsula. Hatched lines indicate presence of harbor seals; numbers refer to the names of locations listed in Table 1. To avoid confusion, the hatched lines were omitted for the north side of the Alaska Peninsula. Dashed inset is detailed in Figure 3.

Kvichak Bay; the north side of the Alaska Peninsula; and the eastern Aleutian Islands from Unimak Island to Samalga Island (Fig. 1).

Aerial surveys were flown on 17-20 June 1975, 9-13 August 1975, 14-20 June 1976, 19-21 August 1976, and 28-30 June 1977 using a Grumman Widgeon (N141R) aircraft chartered from Peninsula Airways, King Salmon, Alaska.

Systematic flights were made along the coast of the Alaska Peninsula and each island of the eastern Aleutian Islands as weather permitted. Sightings of harbor seals were made from altitudes of 100m-150m. Immediate visual estimates of the number of animals present were made of all groups. Photographs of large groups were taken where possible in order to verify visual counts; we used a 35 mm camera with motor drive unit and 105, 135, or 70-210 mm tele-zoom lenses plus automatic aperture control. Overlapping photos were taken if more than one photograph was required for complete coverage. High speed film was used at an ASA of 160 or 200; dark overcast conditions and high travel speeds required shooting at low aperture stops and shutter speeds of 1/500 to 1/1000 sec. In the laboratory, the photographs were projected onto a sheet of white paper, and individual seals were marked as they were counted to avoid duplication. Pups were difficult to observe in the field and to count from slides; thus, they were not included in the total count for any area. These photographic counts replaced the visual estimates for final analysis.

In the aircraft, two to four observers were used. One sat in the copilot's seat and was the primary photographer. Other observers sat behind the forward observer. They made visual estimates of the number of animals present and recorded the position of each sighting, using detailed area charts. Because we were flying island surveys, only

the right side of the aircraft was used for observing. The pilot did, however, prove to be an important observer when animals were seen in the water from the left side of the aircraft.

Surveys were scheduled to coincide with low tides whenever possible; however, weather and the large size of the survey area often resulted in flights occurring at less than ideal times. We also surveyed for northern sea lions (*Eumetopias jubatus*) during this study (Braham *et al.*, 1980); thus, on a few occasions small groups of harbor seals may have been missed near the larger sea lion rookeries and haul out sites.

Surveys were flown during the height of the sea lion breeding period (June-August) when maximum haul out has been reported for this species (Bonnet and Ripley, 1948; Pike and Maxwell, 1958; and Mathisen and Lopp, 1963). This timing corresponds to the expected harbor seal pupping period (Bigg, 1969), although maximum haul out for this species may occur during the molting period from August-October (Pitcher and Calkins, 1977).

The Bering Sea harbor seal population is unique in that it overlaps range with the spotted seal (*Phoca largha*) (Rice, 1977); the two species appear to share habitat from late winter to spring. Most spotted seals are believed to be in the northern Bering Sea by June (Burns and Harbo, 1977); thus, we do not anticipate that a significant number of spotted seals were included in our survey results.

Results and Discussion

Harbor seals were observed throughout the study area either in the water or hauled out on land. Observations were compiled by specific location for three general areas: northern Bristol Bay coast; the north side of the Alaska Peninsula (including Unimak Island) (Table 1); and the eastern Aleutian Islands (Table 2). Totals included harbor seals hauled out and in the water, recorded to the closest haul out site. When a location was surveyed more than once during any survey, the highest count was used.

TABLE 1. Counts of harbor seals by haul out location, observed during aerial surveys from 1975-1977 along the north coast of Bristol Bay and north side of the Alaska Peninsula and Unimak Island. Numbers are maximum count for each location by month. Dashed lines mean the area was not surveyed. Refer to Figure 1 for locating each reference number.

Ref. no.	Surveyed locations	June 1975	August 1975	June 1976	August 1976	June 1977
–	Bristol Bay Coast (north)	90	300	—	—	—
1	Egegik Bay	50	0	70	0	—
2	Cape Greig Area	0	0	1	0	2
3	Ugashik Bay	196	2	163	438	215
4	Cinder River	2867	113	4503	1008	1530
5	North of Port Heiden	0	0	48	0	4
6	Port Heiden	5273	3453	10,548	4782	6222
7	Seal Islands	1137	75	786	241	497
8	Cape Seniavin	10	0	71	0	2
9	Port Moller[1]	6078	1740	7968	1701	4335
10	Cape Leiskof	125	89	199	1	1
11	Izembeck Lagoon[2]	2034	208	559	1204	874
12	Isanotski Islands	368	414	99	511	422
13	Amak Island	14	61	46	14	12
14	Unimak Island	125	0	5	0	0
	Total	18,367	6455	25,066	9900	14,116

[1]Includes Nelson Lagoon.
[2]Includes Moffet Pt.

TABLE 2. Counts of harbor seals by haul out location, observed during aerial surveys from 1975-1977 in the eastern Aleutian Islands. Numbers are maximum counts for each location by month. Dashed lines mean the area was not surveyed. Refer to Figure 3 for locating each area surveyed.

Ref. no.	Surveyed locations	June 1975	August 1975	June 1976	August 1976	June 1977
1	Ugamak Island	—	30	—	—	0
2	Aiktak Island	50	62	—	100	149
3	Rocks N.E. of Tigalda Island	1	40	4	88	130
4	Kaligagan Island	75	50	—	308	94
5	Tigalda Island	0	76	99	349	0
6	Avatanak Island	44	135	78	107	6
7	Rootok Island	68	131	54	387	101
8	Akun Island	20	146	71	179	35
9	Akutan Island	0	24	57	99	13
10	Baby Islands	178	184	149	430	215
11	Unalga Island	72	37	41	161	32
12	Egg Island	0	80	5	28	0
13	Inner Signal Island	—	50	100	490	290
14	Unalaska Island	612	483	156	173	262
15	Umnak Island	8	148	41	415	199
16	Putsoi Island	12	50	—	40	59
17	Ship Rock	2	0	8	7	4
18	Emerald Island	53	227	15	163	217
19	Black Rock	0	0	0	40	—
20	Kigul Island	—	10	—	25	23
21	Vsevidof Island	0	0	—	71	47
22	Breadloaf Island	—	26	—	28	0
23	Samalga Island	—	178	—	129	84
24	Adugak Island	0	60	0	11	0
25	Annaniulak Island	5	39	0	5	4
26	Pancake Rock	0	13	22	115	2
	Total	1200	2279	900	3948	1966

Northern Bristol Bay Coast

Surveys for harbor seals on the north coast of Bristol Bay did not reveal any consistent hauling out areas, although groups were observed on Hagemeister Island (20-200 animals) during both June and August (1975). Small groups (1-5) were observed in the water throughout the coastal area. Alaska Dept. Fish and Game (1973) reported harbor seals present all along the north coast of Bristol Bay, but no areas of high concentrations were recognized. In Nanvak Bay (east of Cape Newenham), just west of our study area, up to 2500 seals have been observed hauled out on tidal shoals (F. H. Fay, pers. comm.). The highest harbor seal count made for the north coast of Bristol Bay east of Nanvak Bay was 300 in August, 1975 (Table 1).

Northern Coast of the Alaska Peninsula

The majority of all harbor seals observed during this study were seen on eight haul out areas along the north side of the Alaska Peninsula: Egegik Bay, Ugashik Bay; Cinder River; Port Heiden; Seal Islands; Port Moller; Izembeck Lagoon; and the Isanotski Islands in Bechevin Bay (Table 1). Animals were also seen at Cape Seniavin, Cape Leiskof, and Amak Island. In addition, seals were observed in the water along the coast near Cape Greig, north of Port Heiden, and Unimak Island (Fig. 1). In these areas, seals haul out on sandbars and shoals exposed during low tides. Only at Amak Island and the Isanotski Islands were animals observed on offshore rocks and volcanic beaches.

The effect of tidal influence on hauling out behavior is important, as evidenced

from the differences in numbers of animals observed at the major hauling areas. More animals were observed at lower tides than higher tides, regardless of whether the tide was rising or falling ($P<0.01$). In June 1976, 25,066 seals were observed on rising tides from 3-4 ft, whereas only 14,116 seals were seen in June, 1977 during rising tides of 8-9 ft, a difference of 57 percent(Fig. 2). Throughout the study area, there was an inverse correlation between tide height and the presence of harbor seals. This effect is consistent with that reported for other areas (Scheffer and Slipp, 1944; Fisher, 1952; Bishop, 1967; and Newby, 1971). Although the movement of animals between years cannot be discounted as an explanation for the differences in number of animals observed among surveys, there is no information to suggest that such movement occurs, and so we assumed that this effect was negligible.

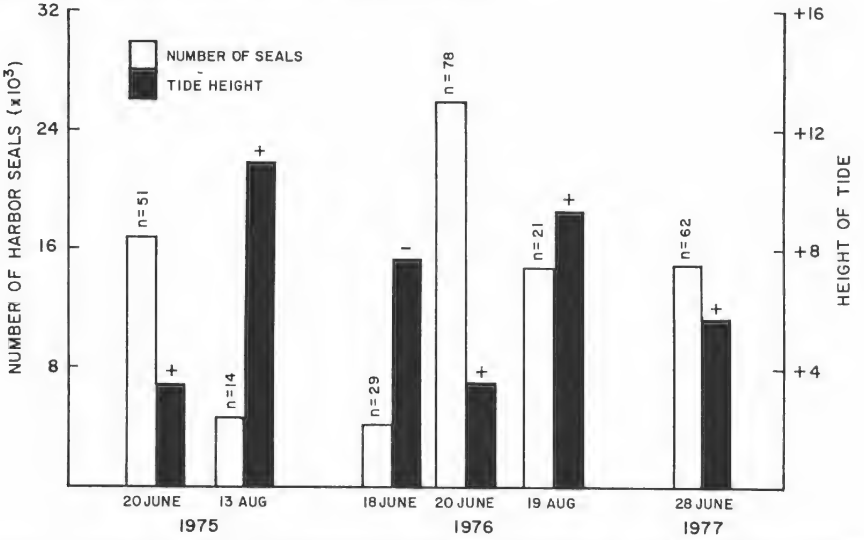

Figure 2. Number of harbor seals hauled out along the north coast of the Alaska Peninsula with respect to tidal conditions, 1975-77. n = number of sightings. ± = tide rising or falling. Tide height was averaged for each survey day.

The counts of harbor seals ranged from about 6000 (August, 1975) to 25,000 (June, 1976). Assuming that 1) these counts were conservative since there will always be an unknown part of the population missed or unobservable in the water; 2) duplicate sightings were minimal; 3) there is little movement of harbor seals among years; and 4) site tenacity in harbor seals is high, then the differences in the numbers of animals present among surveys are believed to be a result of environmental conditions such as tidal influence and visibility. The maximum count of 25,066 should thus be considered a minimum estimate of the number of harbor seals for the north side of the Alaska Peninsula.

Eastern Aleutian Islands

Harbor seals are present throughout the eastern Aleutian Islands (Table 2), with highest concentrations regularly observed on the Baby Islands, rocks off Tigalda Island,

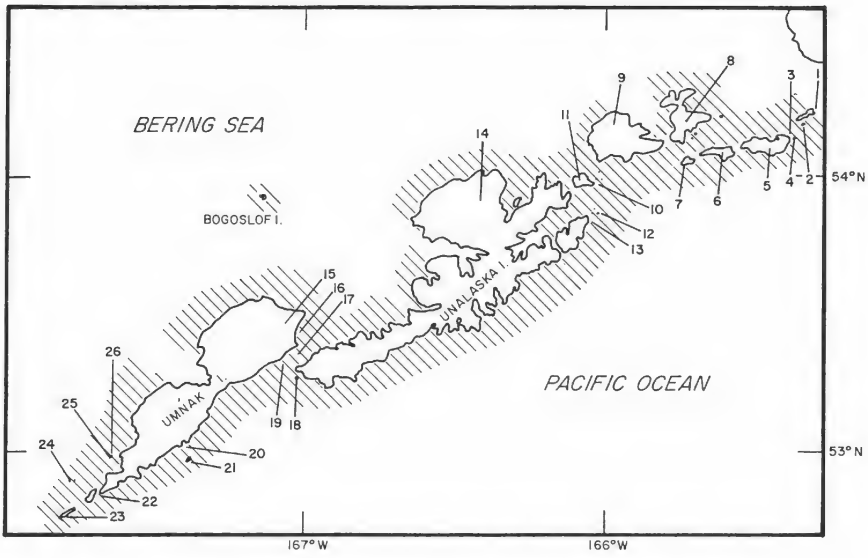

Figure 3. Haul out areas for harbor seals in the eastern Aleutian Islands. Hatched lines indicate presence of harbor seals; numbers refer to the names of locations listed in Table 2.

Rootook Island, Inner Signal, Emerald Island, and Samalga Island (Fig. 3). On Unalaska and Unimak Islands, seals were distributed along the headlands in small groups. The inland waters of these two islands were not surveyed and include Inanudak Bay, Kashega Bay, Skan Bay, Makushin Bay, and Beaver Inlet. Harbor seals have been described as present in these areas (Alaska Dept. Fish and Game, 1973).

Surveying at low tide is important in this area because many of the rocks and offshore reefs where seals haul out are covered during high tide. In June 1975 and 1976, heavy fog on the Pacific side of the islands prevented complete survey coverage and resulted in lower counts than other surveys. Despite this factor, counts in August were higher than in June for any survey year. Whether this result is an artifact of survey conditions or a real condition is not known. The maximum count for the eastern Aleutian Islands for any one survey was 3948 in August, 1976.

Abundance Estimate

Summary counts for each haul out location by general survey area are given in Table 3. The total count of harbor seals by survey ranged from 8734 to 25,966. By using the maximum count for each area and assuming no major movements between areas among survey years, a minimum abundance estimate of 29,314 was derived. We recognize the potential biases in pooling data among years and what effect these biases could have on a "true" estimate. However, the difference between a pooled estimate (i.e., using data for different areas for different years) and the highest count for any one year (i.e., June, 1976) is only 11 percent. Since a greater bias exists in having a low count during any one year because of missed animals, we feel justified in the pooled-estimate pro-

cedure to establish a minimum abundance estimate. Evidence is emerging to suggest that harbor seals may haul out in maximum numbers during the molting period (Pitcher and Calkins, 1977) which occurs in the fall (Stutz, 1967). If harbor seals haul out in greater numbers during September or October than in June or August, then our estimate is undoubtedly low.

TABLE 3. Summary of total counts of harbor seals observed during aerial surveys in the southeastern Bering Sea from 1975-1977. Dashed lines mean the area was not surveyed.

General area	June 1975	August 1975	June 1976	August 1976	June 1977
Bristol Bay (North Coast)	90	300	—	—	—
Alaska Peninsula[1] (North Coast)	18,277	6155	25,066	9900	14,116
Eastern Aleutian Islands	1200	2279	900	3948	1966
Monthly total	19,567	8734	25,966	13,848	16,082

[1]Including Unimak Island.

The north side of the Alaska Peninsula accounted for most harbor seals observed in the study area. Port Heiden, Port Moller, and Cinder River contributed 78 percent of the total for the study area (36 percent, 27 percent, and 15 percent, respectively). The maximum count from these three locations, important breeding sites, was 23,019 animals (June, 1976). This figure represents approximately 8.5 percent of the entire Alaskan population estimate. Apparently, then, these three areas are significant locations for the annual production of harbor seals for at least this part of the species range in Alaska.

Acknowledgments

O. Seibert, President of Peninsula Airways, King Salmon, Alaska, flew the survey aircraft and provided guidance and knowledge of the area under study. C. H. Fiscus was instrumental in developing the surveys.

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Pocket Mouse Population Response to Winter Precipitation and Drought

Abstract

A relationship between autumn-winter precipitation and population of *Perognathus parvus* is demonstrated. Captures are compared to phytomass and monthly precipitation for a drought year and an average year.

Introduction

In the monographic study of a population of Great Basin Pocket mice (*Perognathus parvus*) in the arid shrub-steppe of south-central Washington, O'Farrell *et al.* (1975) identified food as appearing to be "an essential resource" critical to cueing the behavioral and physiological response of the population. Schreiber (1973) thought that cheatgrass (*Bromus tectorum*) is probably the most significant single dietary item used by pocket mice and demonstrated an apparent relationship between increased cheatgrass production and reproductive success in pocket mice. Beatley (1969) concluded that the occurrence or absence of reproduction in desert heteromyids in southern Nevada is correlated with the abundance of winter annuals. Furthermore, she notes that if the amount of autumn rainfall was measured, it was usually possible to predict whether there would be significant reproduction in the heteromyid population in the following spring. In both of these instances, the production of both annual and perennial grasses is dependent on autumn and winter precipitation to recharge soil water and promote plant growth. Therefore, there is an inferred relationship involving precipitation, food production and availability, and population response in *P. parvus*. We attempted to demonstrate the relationship between precipitation and population response by live trapping a pocket mouse population. By comparing our results with the previous studies performed at the same location, temporal trends in the spring population captures were related to the previous autumn-winter precipitation levels.

The study was initiated in April, 1977 in the wake of one of the driest winters on record in eastern Washington. The study was concluded in June, 1978 following a winter with average precipitation. Therefore, a relationship between precipitation and the pocket mouse population would be all the more apparent.

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Study Site Description

The study location is the U.S. Department of Energy's Arid Lands Ecology (ALE) reserve located on the Hanford Site in south-central Washington. The trapping grid is located on a gentle northeast facing slope at the base of Rattlesnake Mountain. The plot altitude is approximately 360 m above mean sea level. The soil type on the study plot is Ritzville silt-loam up to 2.0 m deep overlying basalt. Measurements of precipitation and temperature have been recorded since 1968 at the plot as part of the ALE micrometeorological network (Thorp and Hinds, 1977). The vegetative cover on the plot consists of big sagebrush, bluebunch wheatgrass and other species characteristic of the *Artemisia tridentata/Agropyron spicatum* association in near pristine condition (Daubenmire, 1960). There is very little cheatgrass in the study area (Rickard *et al.*, 1975).

The study site is one of four 9.0 ha plots that were established to study the ecological effects of cattle grazing on small mammals. This former study was a part of the IBP Grasslands Biome Ecosystems Analysis program. Technical Reports Nos. 174 and 243 in this program describe the study site in further detail (O'Farrell *et al.*, 1972 and 1974). The plot used in our study was moderately grazed, but with the cessation of grazing and field trapping in 1975, it was not used for study purposes until the initiation of our project in 1977.

Methods and Materials

The study plot contained a 12 x 12 rectangular trap grid with Sherman live traps placed at 15 m intervals. Each trap slid into a "mailbox" sleeve, and together these were placed under a galvanized metal tent. The purpose of the sleeve and tent was to shade the trap and thus keep a trapped animal cooler in hot weather. Dacron batting was placed in each trap to act as nesting material and to insulate the animal in cooler temperatures. A small handful of "bird" seed was also deposited in each trap to help prevent torpor. We extended the grid perimeter to include one-half the distance between traps, i.e., 7.5 m; the effective trapping area was calculated to be 3.24 ha.

Trapping sessions occurred on weekends at three- to four-week intervals throughout the period of the study. Traps were opened and baited with a peanut butter-oatmeal mixture on Friday evening. Traps were inspected on Saturday and Sunday in the early morning. Hence each trap session consisted of two trap nights with 144 traps open per night, giving a total of 288 trap nights per session.

Captured animals were individually identified by toe amputation. Each animal was inspected to determine species, sex, age class (either juvenile or adult), pelage, reproductive condition, and weight. After inspection and data recording, the animal was released near the point of capture.

Primary productivity expressed as grams per square meter per year was obtained by clip harvest of sixteen 0.5 m^2 circular plots randomly placed in a 9 ha plot adjacent to the plot containing the trap grid. Species were identified in each circular plot, clipped and weighed after oven-drying at 50°C. Two harvests were made in 1978; once in April to obtain a measure of the phytomass of Sandberg bluegrass and early maturing annuals, and once in early June to estimate the phytomass of late flowering perennial grasses and forbs. In 1977, only one plant harvest was made when it became apparent that the severe drought conditions would not permit the usual sequence of plant development and maturation.

Results

Monthly precipitation levels of 12 month periods during 1969-70, 1970-71, 1975-76, and 1976-77 are listed in Table 1. The data indicate that the majority of precipitation falls in the autumn and winter months, October to April. This season has been termed the "bioyear precipitation" (Thorp and Hinds, 1977) due to the heavy reliance of the vegetation on soil water stored during this period of the plant growing season. Thorp and Hinds (1977) noted that the average bioyear precipitation on our plot was about 20 cm. Summation of the bioyear precipitation levels for the years listed in Table 1 shows that 1969-70 (23.2 cm) was an above average season; 1971-72 (18.9 cm) and 1975-76 (19.2 cm) were average seasons; and 1976-77 (4.6 cm) was far below average.

The spring (April+May+June) trapping results of O'Farrell *et al.* (1972 and 1974) for the years 1971 and 1972 are compared with our results in Table 2. The number of traps set each night, the total number of nights in which traps were activated, and the total trap effort (number of trap nights) for this three month period are also compared in Table 2. The data of O'Farrell *et al.* in 1971 and 1972 were not achieved in the same manner as our data of 1977 and 1978. The difference occurs in the total trap effort that took place in the respective two year periods, particularly as affected by the number of traps set per night. In 1971, the initial spring population response was estimated through a total trap effort of 4320 trap nights. In 1972, this figure fell to 2256 trap nights while our effort consisted of 1152 trap nights in both 1977 and 1978. To make the data comparable, we normalized the "traps set per night" (Column A, Table 2) to 144. The spring population response for each year was then multiplied by this normalization factor to give the normalized population levels listed in Column F of Table 2. We believe this is a legitimate calculation since the average home ranges of female and male (*P. parvus*) have been approximated to be 6 and 16 m respectively (O'Farrell, 1975). Thus, in 1977 and 1978 with only 144 traps opened per night, all trappable *P. parvus* may not have been accounted for since the traps were 15 m apart. In other words, once a trap had been filled, that trap was no longer available to pocket mice with over-

TABLE 1. Monthly precipitation (cm) measured at the study site.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.
1969-70	0.8	0.0	4.2	11.8	3.5	1.3	1.6	1.8	0.4	0.0	0.0	0.0
1970-71	1.5	2.1	5.2	3.6	0.5	5.6	0.4	2.5	0.9	0.4	0.8	2.1
1975-76	3.1	3.3	3.0	2.9	3.2	1.9	1.8	0.6	0.3	0.9	1.8	0.1
1976-77	0.4	0.1	0.4	0.5	1.9	1.3	0.0	1.4	1.5	0.2	4.9	3.9

TABLE 2. Summary of April, May, June trapping results for pocket mice at the study site.

Year	A Traps set per night	B Total nights opened	C Total trap effort (A x B)	D Spring captures	E Normalization factor	F Normalized spring captures (D x E)
1971[1]	288*	15	4320	167	0.50	84
1972[2]	188**	12	2256	99	0.77	76
1977	144	8	1152	69	1.00	69
1978	144	8	1152	43	1.00	43

*2 Sherman live traps placed at each of 144 trap sites.
**2 Sherman live traps placed at each of 44 peripheral trap sites; 1 trap placed at remaining sites.

[1]O'Farrell **et al.**, 1972.
[2]O'Farrell **et al.**, 1974.

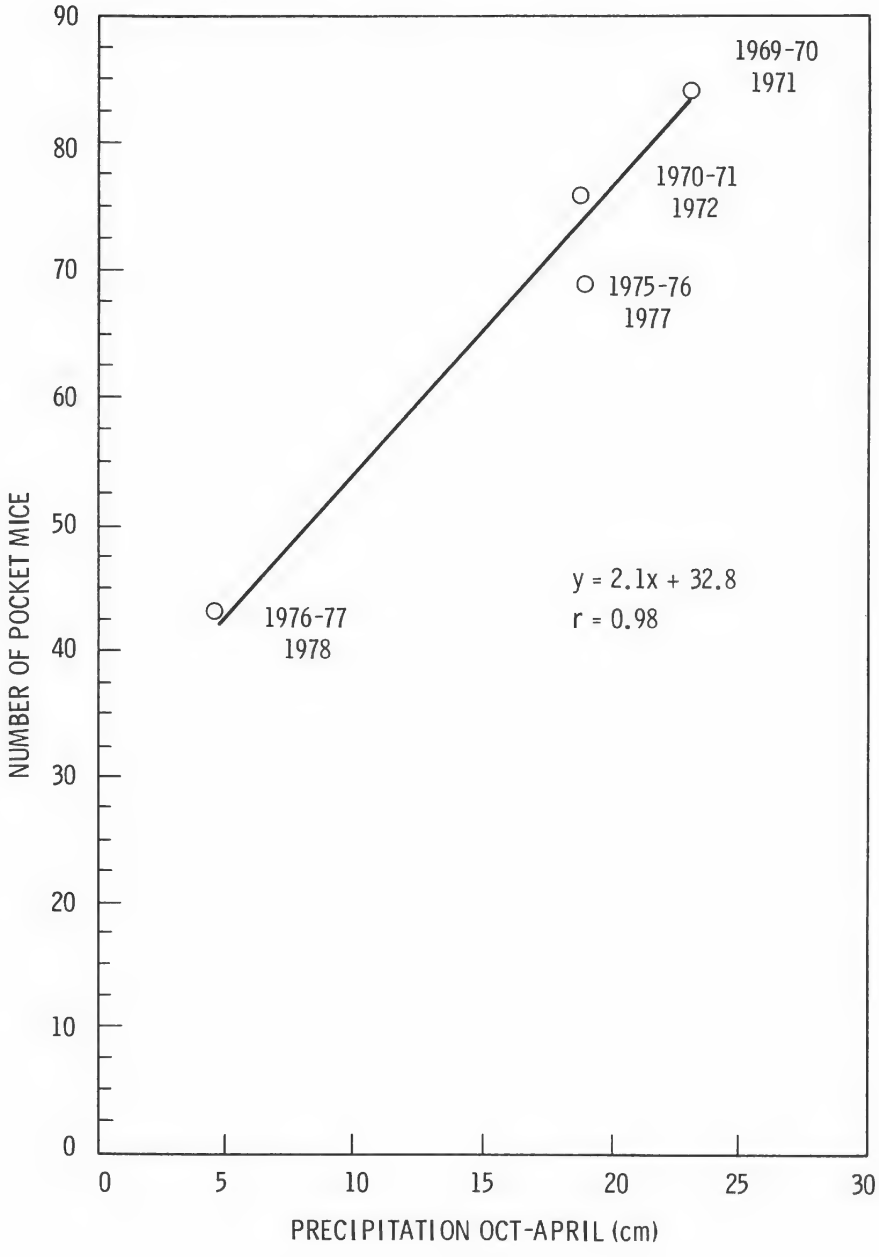

Figure 1. The relationship between the number of pocket mice and October through April precipitation.

lapping or neighboring home ranges to that of the trapped animal. By placing two traps at each trap location and trapping for an extended period of time, O'Farrell *et al.* showed in 1971 that more pocket mice may indeed be captured.

The normalized spring captures are compared to the bioyear precipitation levels of the preceding season in Table 3. These data are plotted in Figure 1, with the *P. parvus* spring captures plotted as a function of the October-April precipitation totals. A regression of the plot yields the following linear equation:

$$y = 2.14\ x + 32.78$$

A calculation of Pearson's correlation coefficient between these two variables gave $r = .98$, indicating a strong relationship between the autumn-winter precipitation and the *P. parvus* captures of the next spring.

TABLE 3. Summary of precipitation during the plant growing season October through April in relation to the trap catch of pocket mice (**Perognathus parvus**).

October-April precipitation (cm)		Normalized **P. parvus** spring captures (numbers)		Reference
23.2	(1969-70)	45	(1971)	O'Farrell **et al.**, 1972
18.9	(1970-71)	76	(1972)	O'Farrell **et al.**, 1974
19.2	(1975-76)	69	(1977)	This study
4.6	(1976-77)	43	(1978)	This study

Discussion

The trappability of the *P. parvus* closely follows the adaptive strategies described by O'Farrell *et al.* (1975); i.e., pocket mice emerge from winter torpor and are readily trapped during the spring when fresh food supplies are probably the greatest. The onset of reproductive activity is coupled with food gathering. These combined physiological drives facilitate trapping of pocket mice in the spring, usually between April and June (O'Farrell *et al.*, 1975). Our trapping results in 1977 and 1978 confirm this observation. Since the spring population size is a function of the reproductive activity/success of the previous summer, and since breeding may be curtailed or encouraged in response to food availability and quality which is in turn a function of bioyear precipitation, the spring captures are a good indicator of the previous fall-winter precipitation level. Conversely, by knowing the fall-winter precipitation total, one may predict the size of the *P. parvus* population in the spring of the following year, if indeed a relationship between fall-winter precipitation level and spring pocket mouse population size does exist.

O'Farrell and co-workers (1975) attempted to quantify a relationship similar to the above by using the Jolly-Seber stochastic model to estimate the *P. parvus* summer population size and then regressing these data against October-April precipitation levels. They, too, observed a linear relationship for the four-year period 1967-70 with a correlation coefficient of $r = .99$. They noted that no correlation is found when the population data are regressed against total annual precipitation. This finding indirectly confirms the notion that fall-winter precipitation is the better indicator of primary productivity and hence food availability for rodent species in arid ecosystems.

Plotting the normalized spring captures against the previous fall-winter precipitation levels also yields a good correlation ($r = .98$). Except for the artifice of normaliza-

tion, the correlation was performed with real capture data and not with modelled numbers as in O'Farrell *et al.* (1975). The purpose of both correlations was the same: to relate the bioyear precipitation level to some indicator of *P. parvus* population size. The good correlation in both instances further supports the hypothesis that *P. parvus* population response is cued by an environmental factor, as discussed specifically by O'Farrell *et al.* (1975) and more generally by Beatley (1969). The factor indicated by this evidence is food. Thus, the strong correlation between an abiotic factor such as precipitation and the response of *P. parvus* is probably mediated by the availability of quality food items such as fresh seeds.

The results of live phytomass harvests are shown in Table 4. The impact of the 1977 drought upon plant productivity is clearly indicated. Only a fraction of the normal phytomass was produced in 1977. However, primary productivity was restored during the 1978 growing season. The 70 g/m^2 of herbaceous phytomass produced in 1978 is much like the range of 61-75 g/m^2 produced in the years 1971-74 (Rickard *et al.*, 1976). The 1978 phytomass consisted of a flush of annual plant growth, especially *Festuca octoflora*, which is a prolific seed producer similar to other annual grasses. *Bromus tectorum*, another annual grass, actually dominates the herbaceous vegetation in disturbed ground at other places in the ALE Reserve, but was sparingly represented in our study plot.

Kritzman (1974) has shown that populations of *P. parvus* on the ALE Reserve are primarily granivorous in the summer and early fall, although insects are consumed prior to the production of seeds. Thus, the above reasoning could be verified by monitoring

TABLE 4. Live herbaceous phytomass measured in the years 1977 and 1978 and expresed as g/m^2/yr.

Taxa	1978	1977
Perennial grasses		
Agropyron spicatum	25.7	3.1
Poa sandbergii	9.4	0.43
Stipa thurberiana	0.73	—
Stipa comata	0.06	—
Perennial forbs		
Astragalus purshii	2.40	1.8
Crepis atrabarba	0.70	0.07
Lupinus laxiflorus	T	—
Calochortus macrocarpus	T	—
Lomatium macrocarpum	T	—
Low shrub		
Erigeron filifolius	22.0	1.9
Phlox longifolia	0.84	1.3
Antennaria dimorpha	—	1.4
Annual grasses		
Festuca octoflora	4.7	—
Bromus tectorum	0.26	—
Annual forbs		
Descurainia pinnata	2.1	—
Draba verna	0.18	—
Holosteum umbellatum	T	—
Sisymbrium altissimum	0.77	—
Plantago patagonica	T	—
Tragopogon dubius	T	—
Total live phytomass g/m^2/yr	69.6	10.0

T=Trace Amount

the levels of seed production to study correlations not only with population response in *P. parvus* but with levels of autumn-winter precipitation. Confirmation of such a relationship would provide a predictive tool to estimate the size of pocket mouse populations by measuring the fall and winter precipitation. Nevertheless, the chemical mechanisms that trigger the reproductive response in the pocket mouse population remain obscure.

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Factors Influencing Smallmouth Bass Production in the Hanford Area, Columbia River

Abstract

Forty radio frequency transmitters and 120 dart tags were used to monitor movements of adult smallmouth bass (*Micropterus dolomieui*) in relation to water level fluctuations in the Columbia River at Hanford, Washington, in 1976 and 1977. Adult bass spawned from April through June in warmed sloughs and backwater areas bordering the Columbia River. They returned to the main river channel after spawning in August, 1976 and in late June, 1977. Bass movement appeared to be influenced by water level fluctuations, water depth, current, and available forage organisms. Radio-tagged bass traveled a maximum of 61 km, and dart tags were returned from as far as 63 km.

Spawning success of adult bass was estimated at three study areas: White Bluffs, Hanford, and F Area sloughs. Spawning was adversely influenced by high river levels, which flooded nest sites with cool water and caused other perturbations. Spawning success was relatively poor in 1976, a high-water year, and relatively good in 1977, a low-water year. Loss of juvenile bass due to entrapment, predation, thermal and oxygen stress, and desiccation was monitored during the summer in several temporary ponds created by fluctuating river flows. Adverse ecological factors were related, for the most part, to seasonal water regimes in the Columbia River during the spawning period, and to interseasonal fluctuations in flow levels from hydroelectric power generation at Priest Rapids Dam.

Introduction

Studies on smallmouth bass (*Micropterus dolomieui*) were initiated at Hanford to evaluate the ecological effects of water level fluctuations. Water flow in the free-flowing Columbia River below Priest Rapids Dam varies sharply in response to power peaking and flood control demands. Preliminary observations in 1976 indicated that adult and juvenile smallmouth bass were subject to entrapment, desiccation, and predation during acute, short-term fluctuations. Further, bass nests were apt to be impacted by dehydration, siltation, and abrupt temperature changes during the spawning season.

During 1976 and 1977, smallmouth bass in the Hanford area experienced two contrasting water regimes (Figure 1). High flows prevailed in the spring and summer of 1976, and water levels in the Columbia River did not recede to normal summer lows until late September. Low flows existed throughout the spring and summer of 1977, and water levels in bass spawning areas fluctuated less from power generation at Priest Rapids Dam during high-low demand periods. The contrasting flow patterns presented different environmental conditions during and after seasonal spawning of smallmouth bass.

This report summarizes observations and data on residence periods of smallmouth bass in spawning areas at Hanford, spawning activity, movements during and after spawning, and entrapment and desiccation of juvenile bass. Estimates are provided on relative

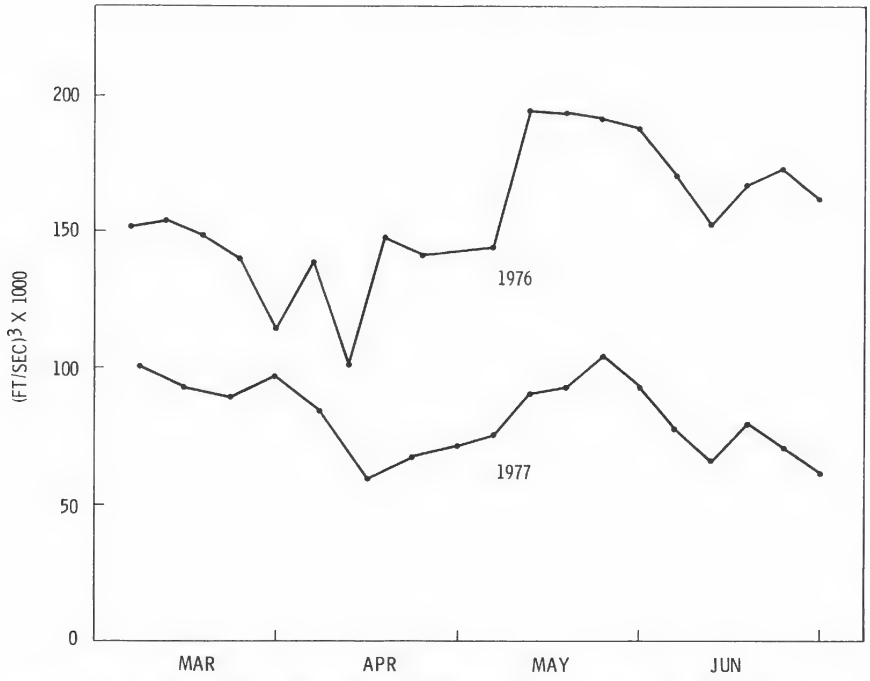

Figure 1. Mean weekly water flows from Priest Rapids Dam from March through June 1976 and 1977. The contrasting flow regimes were associated with the amount of water available seasonally from upriver runoff and regional power generation requirements.

spawning success for 1976 and 1977, and some effects of water level fluctuations are evaluated.

Methods and Materials

Smallmouth bass were observed and monitored from March to mid-October of 1976 and 1977 in White Bluffs Slough, F Area Slough, and Hanford Slough (Figure 2). Movements of adult bass were monitored in the Columbia River from Priest Rapids Dam to below the confluence of the Snake River. Observations included surveys and sampling of bass populations by electro-fishing, seine, and hook and line gear. Crayfish traps, trapnets, and electro-fishing were used to evaluate abundance of forage species available to bass. Field observations gave information on bass spawning behavior and reproductive success at the study sites. Adult bass were collected to determine seasonal presence and abundance in each study area, and to provide specimens for tagging with radio transmitters and dart type (Floy)[1] tags (Figure 3). Fry mortalities and entrapped adult bass were estimated from sightings and the number of bass collected at several entrapment areas. Losses of adult and juvenile bass from stranding and dehydration were estimated by counting actual mortalities.

Seven adult bass in 1976 and 40 adult bass in 1977 were tagged with radio frequency transmitters to monitor spawning behavior and movement. One hundred and twenty additional bass were tagged with dart tags to supplement radio-telemetry data. The trans-

[1]Use of brand name does not imply endorsement.

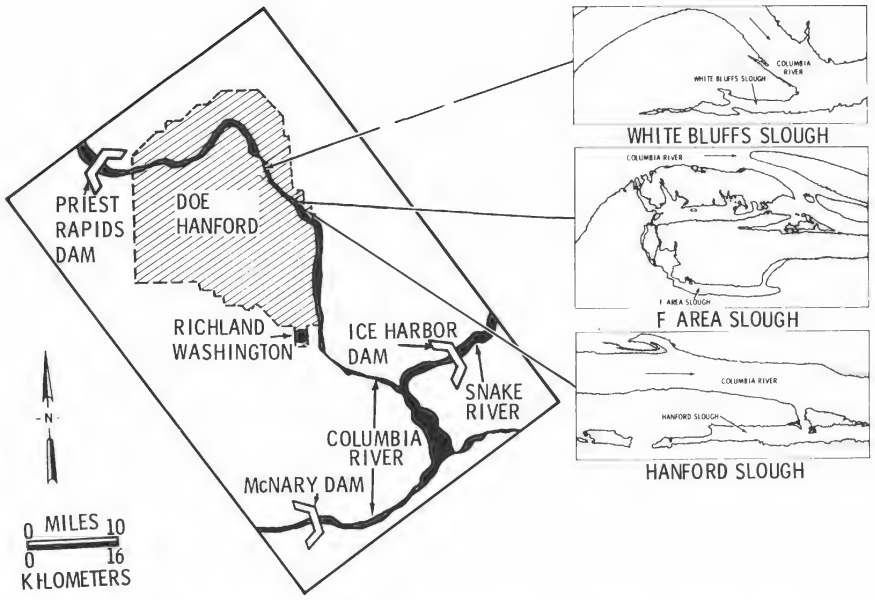

Figure 2. Diagram of the Columbia River at Hanford, showing specific locations of the three study sloughs where spawning and residence times of smallmouth bass were examined.

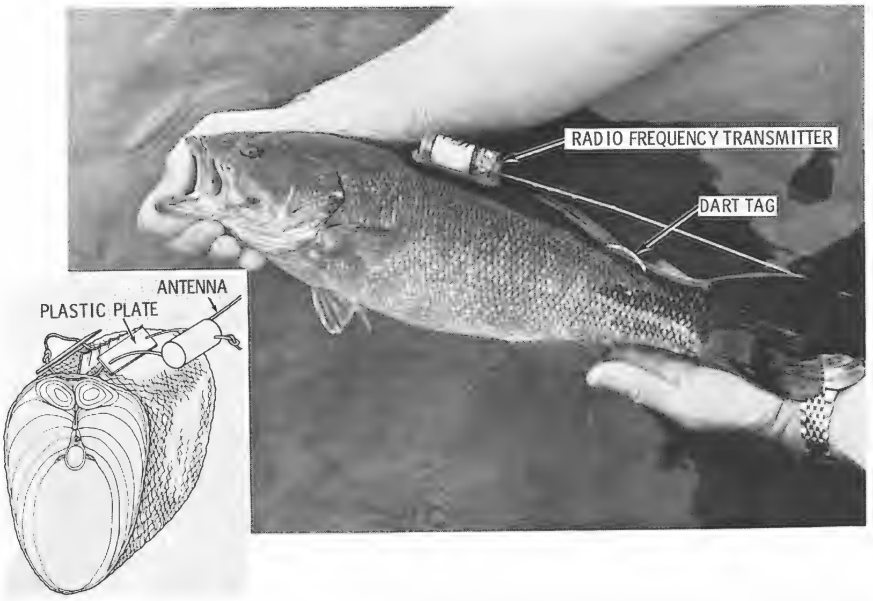

Figure 3. Smallmouth bass displaying attachment of both a radio transmitter tag and dart type tag. Inset: Cross section of fish showing method of attaching a radio transmitter with plastic plates to restrict abrasion.

mitters and receivers were manufactured at the University of Minnesota Bioelectronics Laboratory at Cedar Creek (Tester and Siniff, 1976). Each transmitter was encased in epoxy, which also anchored teflon-coated attachment cables. Transmitters were 50.8 mm long and 15 mm in diameter, and weighed 19.3 $\pm$ 0.5 g in air (about 0.25 gm in water). The plastic coated wire antenna was 30.1 $\pm$ 4 mm long. Battery life of transmitters averaged 4.0 $\pm$ 0.5 mo.

Radio tags were attached by inserting attachment cables with a surgical needle through each fish below the dorsal fin (Figure 3, inset). A small flexible plastic plate on each side allowed firm attachment of each transmitter and minimized abrasion. Dart tags were placed below the posterior dorsal fin (Figure 3). All tagging incisions and capture abrasions were treated with malachite green to retard bacterial infection. Standard length, general condition, sex (if possible), and estimated weight of fish were also recorded before release.

Radio-tagged adult bass were monitored with antennas and receivers mounted on a boat or truck two or more times weekly, and fish locations were recorded on a site or river map. The receivers operated on a carrier frequency of 53 MHz and could distinguish 100 different crystal-tuned transmitters. Since signal strength decreased with swimming depth, the approximate depth inhabited by individual fish could be determined. Signal attenuation was calibrated in the field by lowering several radiotags to known depths.

Results

1976 Spawning Data. Adult smallmouth bass entered the study sloughs from the Columbia River in mid-March as water temperatures increased, and they remained there until August. Gravid females were collected through mid-August. Males guarded nests until late July; no nesting or guarding activity was observed after July. Radiotelemetry data on seven adult bass at White Bluffs Slough confirmed that fish would carry the transmitters and could be traced, and these fish provided initial information on bass post-spawning movement. Most adult bass did not return to the Columbia River after spawning until late August.

Field observations indicated poor spawning success. Eggs failed to hatch in several bass nests, and relatively few swarms of fry were observed at the three study sites. Five bass nests were located and observed at White Bluffs Slough from the time of egg deposition until fry left the nests. Two of five nests showed signs of partial hatching. However, less than 50 swimming fry were observed in the area. A successful smallmouth bass nest will normally produce about 2000 fry (Scott and Crossman, 1973), although the range can extend from 500 to 11,000 (Carlander, 1977).

1977 Spawning Data. Adult smallmouth bass began inhabiting White Bluffs and Hanford sloughs in mid-March, and F Area Slough in early April. Spawning began in late April and continued into July; several adult bass remained in the study areas through late July. F Area Slough was inundated by high water released at Priest Rapids Dam for a short period (2-6 days) in early April, which permitted sexually mature bass to enter the area. As flooding receded, the entrance channels closed and bass were trapped in the slough. These fish remained confined from mid-April, 1977 through the following winter, and could not return to the mainstream Columbia River until rising water in March, 1978 permitted their departure.

Smallmouth bass spawning appeared successful at all study sites that were not

subjected to fluctuating high water flows from the Columbia River during the spring and summer of 1977. Bass entrapped at F Area Slough showed the best reproductive success and 30,000 to 40,000 fry were produced, based on estimates of abundance in over 80 swarms of fry observed. Bass spawning at White Bluffs and Hanford sloughs appeared less successful. Yet, an estimated 10,000 to 15,000 bass fry were detected at each site.

Tagging Data. Forty smallmouth bass carrying radio transmitters (15 fish at White Bluffs, 15 at F Area, 10 at Hanford slough) were monitored from late March to mid-October, 1977. Tagged bass averaged 37.2 $\pm$ 2.5 cm standard length. Although spawning began in late April, and the peak egg hatch was complete by mid-June, several tagged fish remained in the sloughs until July. All mature bass at F Area were trapped throughout transmitter battery life because low water prevented their return to the Columbia River.

After leaving the spawning areas, radio-tagged adult bass remained near the mouth of White Bluffs and Hanford sloughs for one to two weeks. Tagged bass at White Bluffs remained in the pool adjacent to the slough mouth, and favored deeper water at depths of 6-16.5 m. Tagged bass at Hanford Slough tended to disperse downstream. Typical movements of one fish at each location are shown in Figure 4. A maximum distance of 61 km downstream was recorded (Table 1).

Bass dispersing from the Hanford Slough stayed near midstream islands, shorelines, and in backwater areas directly connected to the Columbia River. Dart tags from Hanford Slough fish were returned by fishermen from as far as 63 km downstream. Movements of fish carrying dart tags were similar to those carrying radio transmitters. All tagged fish recaptured were from the Columbia River.

Entrapment and Desiccation. During 1976 and 1977, entrapment and subsequent

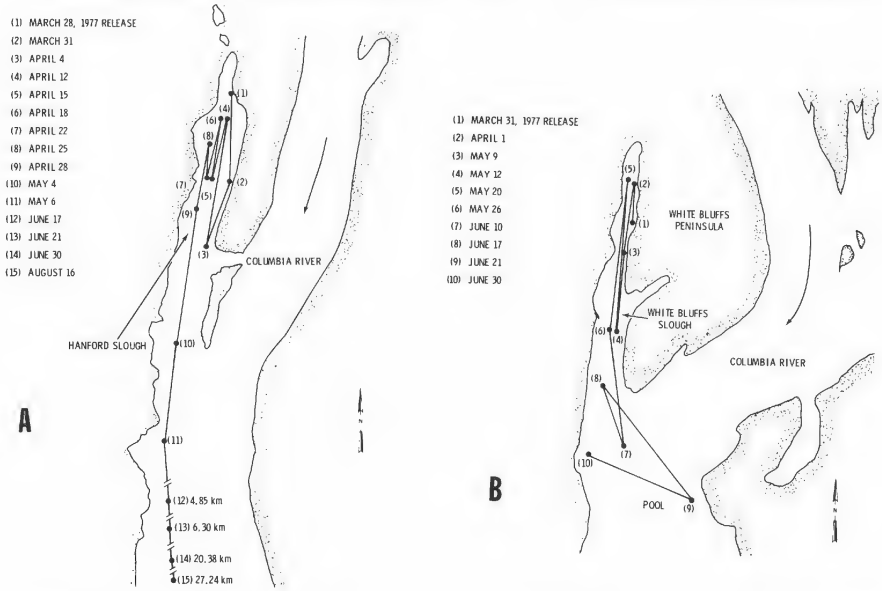

Figure 4. Example showing movement of a radio-tagged adult smallmouth bass at Hanford Slough and White Bluffs slough (A, tagged fish # 705; B, tagged fish #250).

losses of smallmouth bass from desiccation, predation, or thermal stress were monitored in several different ponds and flooded areas. Entrapment was due to daily, weekly, and seasonal fluctuations in water level.

TABLE 1. Maximum distances moved by radio tagged adult bass monitored from April through September, 1977 at Hanford.

Maximum Distance Moved (km)			
WHITE BLUFFS SLOUGH[1]		HANFORD SLOUGH[2]	
1.11	1.30	7.78	1.30
1.48	1.30	11.12	2.41
1.30	1.48	61.00	9.45
1.67	1.48	27.24	7.60
1.48	5.74	7.60	
1.30	1.67		
1.85	1.67		
Mean=1.77 km		Mean=15.06 km	
Var(Mean)=0.10		Var(Mean)=39.16	
SE=0.31		SE=6.26	

[1]One bass was entrapped 12 May 1977 until tag failure on 6 September 1977.
[2]Tag on one bass failed in 11 days operation when the fish had moved 0.93 km down river.

At the head of F Area Slough, a creek 2.6 km long was created in 1976 by high water entering the north end of the peninsula and flowing south. Several temporary ponds were created in the creek where adult and yearling smallmouth bass were later trapped as the water level declined (Figure 5). At the extreme north end of the creek, a large pond about 100 x 800 m (maximum depth, 2.3 m) was formed that trapped an estimated 150 to 250 adult and yearling smallmouth bass. The fish eventually died from terrestrial predators and desiccation in early October, 1976.

Another temporary pond at F Area Slough ($\sim$ 2 m deep) contained 80 to 100 yearling smallmouth and largemouth bass (*Micropterus salmoides*) in September, 1976. The fish died when the pond drained in late July, 1977. A third pond ($\sim$ 0.35 m deep) near the north end of F Area trapped an estimated 80 yearling largemouth and smallmouth bass. These fish died during the winter from freezing and predation.

At the south end of F Area Slough, a large slack-water area ($\sim$ 400 m x 200 m) is formed as the basin bends east towards the outlet. In 1976, several bass nests in the slack-water area each produced 200 to 300 fry. However, shortly after the fry emerged and moved to shoreline areas, discharges from Priest Rapids Dam caused the water level to rise and flood a recessed grassy area behind a high bank. About 125 to 150 temporary ponds of various sizes were formed. Smallmouth bass fry were observed to disperse through the flooded grassy area (Figure 6). Receding water isolated the ponds, which dried within 24 hr. On the next day, only six surviving bass fry were found in a slack-water area in the adjacent Columbia River.

Columbia River water levels remained higher than normal until late September of 1976. One large pond (440 m x 100 m x 4 m deep) at the north end of Hanford Slough became separated from the main slough as the water dropped. The pond contained an estimated 100 to 200 adult smallmouth and largemouth bass, and it remained isolated from the Columbia River until April of 1978. Evaporation of water over this period reduced the pond to one-fourth of its original size. Over the 18 month entrapment period, several collections were made of adult bass and fish food organisms in the pond. Available forage organisms rapidly disappeared and the trapped population showed severe

Figure 5. Aerial photograph of the Columbia River and adjacent F Area slough. The 0.6 km square area contains an estimated 340 small ponds where young bass and other fish were entrapped by fluctuating water levels. The series of checked ponds in lower left are the remnants of a creek that flowed during high water, and stranded adult and juvenile bass as water levels declined.

malnutrition, manifested by pronounced loss of weight and narrowing of the body. By March of 1978, intensive sampling produced no bass, indicating total mortality.

Discussion

Numerous environmental factors affect reproduction of smallmouth bass. According to Cleary (1956), a 45 day post-nesting period is required for smallmouth spawning in Iowa streams. Moreover, when air temperatures dropped from 23.9 to 11.1°C and remained low for 10 days, bass abandoned their nests. Eggs became infested with fungi and lost their adhesiveness, and an increase in water level of only 15 cm swept dead eggs away. Renesting began when adverse conditions subsided, but perhaps not by the original spawners. Emig (1966) summarized data showing that smallmouth bass move into spawning areas at temperatures from 4.4 to 15.6°C, and spawning activity commences at temperatures from 14.4 to 21.2°C; but a drop in temperature will cause nesting to

Figure 6. A grassy area at the south end of F Area slough where juvenile fish, including bass fry, were entrapped by fluctuating water levels.

stop. Webster (1948) noted that eggs developing at 18.3°C in the laboratory and transferred at 0, 1, 3, and 4 days after fertilization to 10.0 and 23.9°C were not adversely affected. Thus, developing bass eggs are resistant to temperature changes over a broad but finite range; more extreme fluctuations will cause mortality from acute thermal shock.

Adult smallmouth bass typically spawn at Hanford in late spring and early summer, after moving into slough areas in April and May. The primary stimulus for this movement appears to be water temperature, which is higher in sloughs during spring than in the main channel of the flowing Columbia River. Henderson and Foster (1956) reported that cold water flushing through slough spawning areas in the Hanford area apparently prevented hatching of bass eggs; they indicated that water temperatures of 12.8 to 15.6°C prevailed during spawning.

Acute changes in water level in the Hanford area may influence reproductive success of smallmouth bass in several ways. Warmer slackwater areas used by spawning bass become flooded with cold water, which retards or halts egg development. Sudden, strong currents may cover eggs with silt and wash larvae from nests. Falling water levels may drive guarding male bass away from nests, permitting predation by other fishes and limiting water circulation over the eggs. During extreme declines in water levels, bass nests may be exposed to air and desiccate. After leaving the nest, bass fry are still affected by fluctuating water levels as they seek forage and cover in shoreline areas. Many fry are trapped or stranded by receding water in small ponds where they are also subject to rising temperatures and predation by birds.

Spawning of smallmouth bass at Hanford is influenced by Columbia River water levels that are reflected within slough spawning areas. Flows in the mid-Columbia River

vary seasonally from year to year, depending on the amount of water available in upriver watersheds. At Hanford, flows also vary daily and weekly in response to release at Priest Rapids Dam during the annual periods that adult bass are spawning. Interseasonal daily and weekly changes in river flow volumes have become more acute in recent years with increased emphasis on regulating flow in response to regional power demands. Unfortunately, stability of water levels in spring and early summer is necessary for successful spawning of smallmouth bass (Watson, 1955).

High spring flows that persisted in 1976 at Hanford resulted in colder water temperatures in slough areas, which explains the extended residence time of adult bass and delayed spawning. Male smallmouth bass remained guarding nests until mid-July, and some females remained gravid as late as mid-August. In contrast, bass spawning in 1977, when water levels during the spring were low and the slough areas relatively warm, appeared relatively successful. Subsequently, less severe water level fluctuations in slough areas accounted for greater egg hatch and fry survival. The enclosed F Area Slough, which experienced no water fluctuations during or after bass spawning in 1977, contained the largest number of fry.

Habitat preference (Munther, 1970), availability of prey, and river flows levels may account for differences in movement of adult bass after spawning. Generally, adult smallmouth bass tend to restrict their movements during a single season. In the Snake River, the home range of most smallmouth bass is a single pool or an area of similar size. However, apart from straying, interseasonal movements of bass in the Snake River are partially a function of continuous suitable habitat, or of the distance and harshness of the areas between suitable habitats (Munther, 1970). At Hanford, the factors influencing postspawning movements of adult bass still remain uncertain.

Our radio-tagging data indicate that adult bass in White Bluff Slough move to deeper portions of the Columbia River after spawning. Bass that spawned in Hanford Slough did not have this option because the Columbia River directly below the outlet is swift flowing and shallow. Slackwater areas and greater depths exist about 3.2-3.8 km below Hanford Slough, and a few tagged bass traveled to and remained in this area after spawning. Several monitored fish dispersed further downstream. Dart tags were returned by fishermen from areas where radio-tagged fish had been or were still present.

Entrapment and subsequent mortalities of adult, juvenile, and 0-age smallmouth bass were recorded in several temporary ponds in 1976 and 1977. Losses were due to desiccation, thermal stress, malnutrition and predation. Although mortalities in field situations are difficult to quantify, bass fry appear especially vulnerable to fluctuating water levels. Fry disperse among aquatic plants along the shoreline shortly after they emerge from the nest, and move deeper into grassy cover as water levels rise. When the water recedes, many fry are trapped and eventually perish. Water fluctuations sufficient to cause this effect are usually rapid and occur within a 24 hr period. A portion of each year's bass hatch in the Hanford area is apparently lost in this manner.

Entrapment ponds persisting 1-18 mo contained several hundred adult, yearling smallmouth and largemouth bass in the F Area (excluding the main study slough), Hanford, and White Bluffs sloughs. Many fish were eventually lost to desiccation, thermal stress, or predation, or they suffered malnutrition as food organisms were depleted. This type of entrapment results from a relatively high spring runoff, as in 1976, followed by one or more years of low water.

Henderson and Foster (1956) noted that the overall success of bass spawning at Hanford was very poor in 1951, 1952, and 1953. They attributed this fact largely to fluctuating water stages and temperatures during the spawning season. Our observations support their assessment and identify a number of other environmental factors influencing the survival of juvenile bass. For the most part, adverse factors are related to seasonal water regimes in the Columbia River during the spawning period. Hydroelectric generation at Priest Rapids Dam, completed in 1959 above Hanford, now also influences bass production by causing acute fluctuations in water level when responding to daily and weekly peak power demands.

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Size and Age of the Tube-snout (Aulorhynchus flavidus) in the Yaquina Estuary, Oregon

Abstract

Aulorhynchus flavidus were collected throughout the year with hatching probably occurring from October through June. Most (99 percent) were collected in eelgrass and not in the upper intertidal. Adults exhibited a unimodal length-frequency distribution and a multi-modal weight-frequency distribution, which indicates that adults were of several age classes.

Introduction

The tube-snout is distributed from Baja California to southeast Alaska (Hart, 1973). Limbaugh (1962) has previously examined the life history of this species in California. Marliave (1976) reported on larval development and proposed a theory for drift dispersal of eggs. Here, I examine length-frequency, weight-frequency, and length-weight relationships to determine if adults belong to one age group as suggested by Limbaugh (1962).

Methods

The 15.8 km^2 Yaquina estuary (44° 38′ N, 124° 03′ W) is located on the central Oregon coast. To sample shallow-water (0.4-0.7 m deep) estuarine fishes (Bayer, 1979b), I used a beach seine (3.0 m long and 1.1 m high with a 10 mm stretched mesh) to capture tube-snouts from August, 1975 to July, 1976. The seine was designed to prevent rolling in eelgrass (*Zostera marina*) and is described elsewhere (Bayer, 1979a). Each sample was composed of a series of 10 hauls, each approximately 30 m long. Seining was in either an eelgrass bed (−0.2 to +0.4 m above Mean Lower Low Water, MLLW) (Bayer, 1979c) or in the upper intertidal over mudflats (0.9 to 1.3 m above MLLW) at embayment areas 2-3 km from the mouth of the estuary. After capture, total length of each fish and wet weight of most fish were recorded. Breeding males can be distinguished by red pelvic fins (Hart, 1973), and I began distinguishing males in January. In this note, all length measurements are total length unless otherwise noted.

Results and Discussion

Although approximately equal efforts were expended in seining in eelgrass and in the upper intertidal, only one of 135 tube-snouts collected was found in the upper intertidal.

Aulorhynchus flavidus were collected every month of the year, but were most abundant in January ($\bar{x}$=7.2/sample, N=5 samples). However, even in January tube-snouts only had a mean density of 0.012/m^2.

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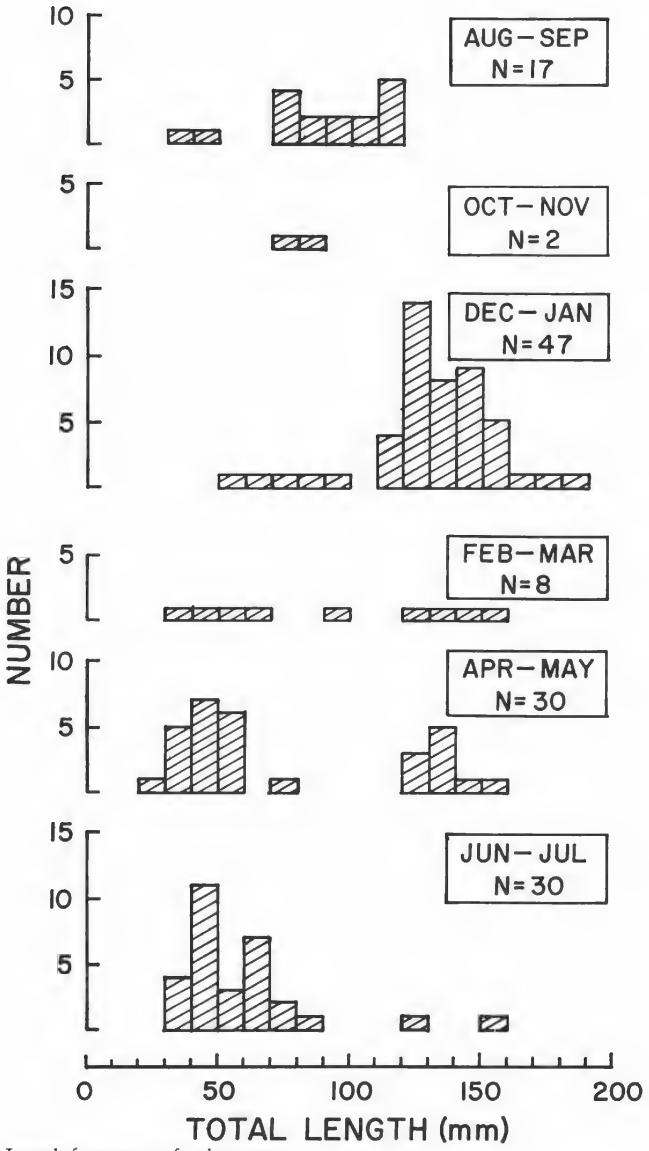

Figure 1. Length-frequency of tube-snouts.

After I began distinguishing breeding males in January, I found a sex ratio of 1 female: 3.6 breeding males (N=23) for fish over 110 mm (probably adults; see Limbaugh, 1962), and in April through July, I found only one female and 11 males. In contrast, Moffett in Hart (1973) found that females outnumbered males during spawning by as much as 10 or 20 to 1, and Limbaugh found females outnumbering males 2.9:1.

Tube-snouts 40 mm or shorter were most abundant from April through July (Fig. 1)

and were also found in August and February. Marliave (1976) indicated that tube-snouts grew to 40 mm within two months of hatching, so hatching in the vicinity of the Yaquina could have occurred from October through June with peak hatching from March through May. This finding indicates an extended period of spawning which was also found by Limbaugh (1962) in California.

The shortest tube-snout was 27 mm long and weighed less than 0.2 g; the longest tube-snout was a 188 mm (13.4 g) female that was longer than previously recorded tube-snouts (177 mm, Hart, 1973). Most large (> 110 mm) specimens were collected in December and January (Fig. 1). Most (53 percent) weighed less than 1.5 g, and 93 percent weighed under 5.0 g. Males ranged from 125 mm (2.7 g) to 150 mm (4.9 g), whereas Limbaugh (1962) found males ranging from 121-153 mm standard length (SL).

It was not possible to calculate a length-weight relationship adequate to predict weights accurately of tube-snouts throughout the length range. For 31 individuals distributed evenly along the length range, the equation was log W=–6.79 + 3.43 log TL (r=.97) (Fig. 2). Only two fish weighed more than 7.0 g, so this equation underestimated the weight of the largest tube-snout (e.g., predicted 11.0 g, actual 13.4 g). For 59 tube-snouts longer than 110 mm, the equation was log W=–8.12 + 4.06 log TL (r=.96), which better predicted the weight of the largest fish (predicted=13.0 g), but was not adequate for the smallest fish. In contrast, for 18 fish less than 110 mm, the equation was log W=–4.05 + 2.04 log TL (r=.70), with a predicted weight for the largest fish of 3.9 g.

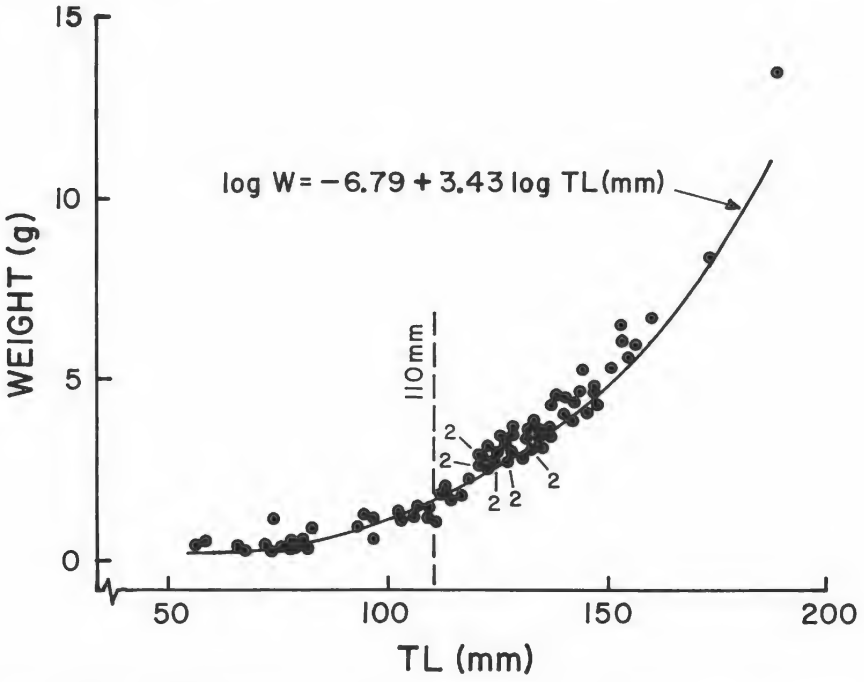

Figure 2. Tube-snout length-weight relationship. Regression line calculated from measurements of 31 fish evenly distributed along the length range.

Length-frequency data (Fig. 1) indicated a unimodal distribution for tube-snouts longer than 110 mm. The mean of fish longer than 110 mm was 136 mm in December and January and in April through July. Similarly, Limbaugh (1962) found a unimodal length-frequency distribution for male and female tube-snouts with males averaging 12 mm shorter than females, but the mean length of fish in his sample was longer, 143 mm SL.

Limbaugh (1962) suggested that the adult unimodal length-frequency distribution indicated that either adults were of a single year group, or that growth ceased after maturity. He suggested that a single age group was more plausible. However, the weights of tube-snouts within the Yaquina unimodal distribution (Fig. 1) were increasing exponentially (Fig. 2) so that the longest individuals in the distribution weighed five times as much as the shortest individuals over 110 mm. Further, weight-frequency data in December and January when most large tube-snouts were collected indicated a multimodal distribution for tube-snouts longer than 110 mm (Fig. 3). On the basis of both length-weight-frequency data (Figs. 1 and 3), adults apparently were of several age groups; although length appears to remain relatively constant after becoming an adult, weight does not.

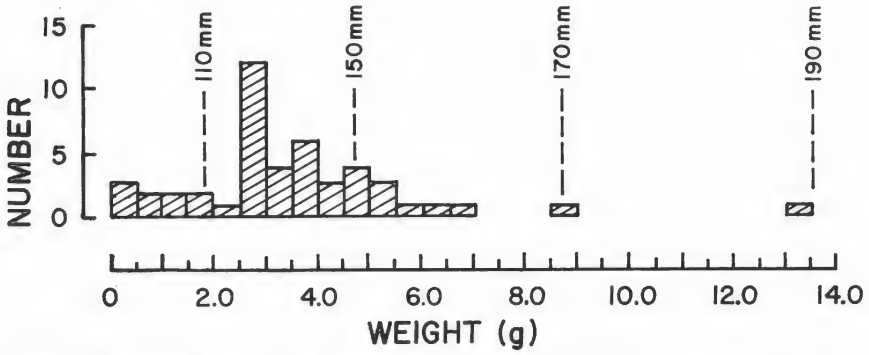

Figure 3. Weight-frequency of 48 tube-snouts in December and January. Frequency for 0.5 g intervals. Vertical lines represent total length for a given weight based on length-weight relationship from Figure 2.

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